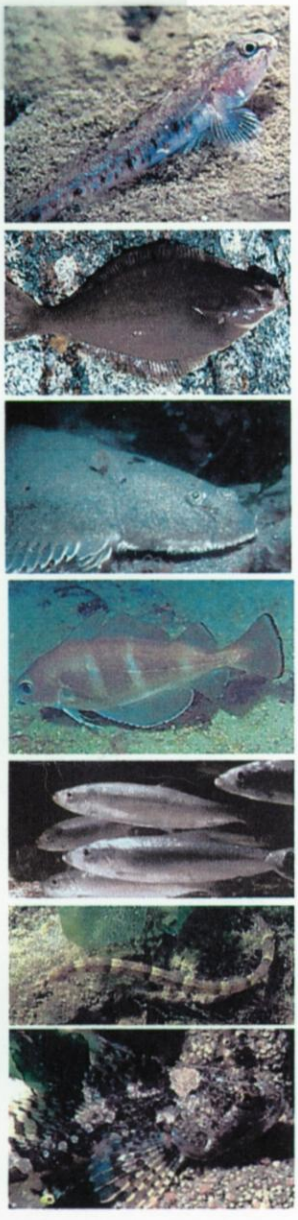
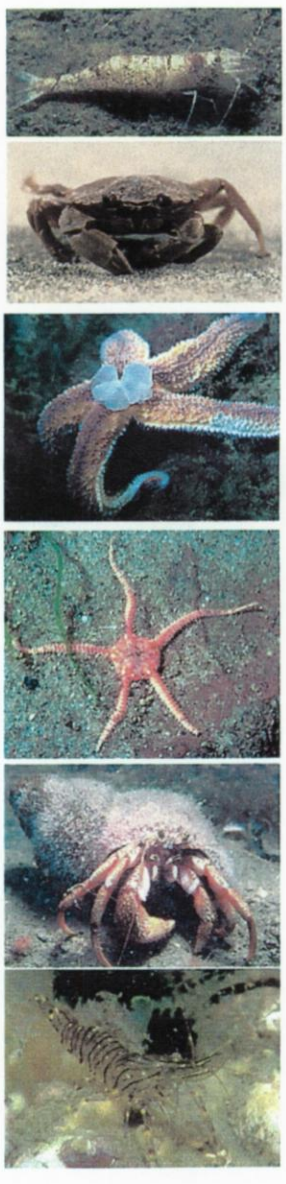
UNIVERSITEIT GENT
Faculteit Wetenschappen

MARINE BIOLOGY SECTION
GHENT UNIVERSITY, BIOLOGY DEPARTMENT



The demersal fish and macro-invertebrate assemblages of the Westerschelde and Oosterschelde estuaries (Southern Bight of the North Sea)

De demersale vis- en macro-invertebraten gemeenschappen van de Westerschelde en Oosterschelde estuaria (Zuidelijke Bocht van de Noordzee)



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Proefschrift voorgelegd
tot het behalen van de graad van
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Marine Biologie
Vakgroep Biologie

This is about a man and a fish.

This is about dramatic relationships between a man and a fish.
The man stands between life and death.

The man thinks.
The horse thinks.
The sheep thinks.
The cow thinks.
The dog thinks.

The fish doesn't think.
The fish is mute.
Expressionless.

The fish doesn't think,
Because the fish knows
Everything.

The fish knows everything...

Iggy Pop (Arizona Dream)

... and I see man

as being like a fish
passing through a huge city.

The fish doesn't understand
anything about the city.

He's just floating through it...

Emir Kusturica (Arizona Dream)

Dankwoord

'Een doctoraat is nooit af'. Een zin die ik meerdere malen gehoord heb in de 13 jaar die dit doctoraat overkoepelen. *Edoch*, met die paar jaar extra is het toch een beetje 'meer af' naar mijn gevoel. Ik moet hierbij in eerste instantie mijn promotor Prof. Dr. *Magda Vincx* bedanken, niet in het minst voor de mogelijkheid die ze bleef bieden om op de één of andere manier aan dit doctoraat te kunnen werken. Magda, we hebben meerdere keren gebotst, en de problemen zijn steeds opgelost geraakt, en je ziet: 't is der toch van gekomen, bedankt.

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Co-promotor Prof. Dr. *Carlo Heip*, en het Centrum voor Estuariene en Mariene Ecologie (CEME, Yerseke, Nederland) in het algemeen, hebben het visonderzoek in Gent blijven steunen. Nogal wat contracten en contacten zijn er gekomen via Carlo en 'zijn' Nederlands instituut. Hopelijk blijft dit een vruchtbare samenwerking. En alhoewel we het niet altijd eens zijn over de manier van aanpak, je wetenschappelijk inzicht heeft mij zeker anders doen kijken naar 'management' van eender welk systeem.

Hierbij dient zeker ook de logistieke ondersteuning via de Luctor (en de Riekus) vermeld te worden. Zonder *Co van Sprundel* en *Wim Röber* als schippers en *Piet de Koeyer*, *Hans Francke* en *Co Verschuure* op het dek, zou er niet veel vis gevangen zijn. In het bijzonder wil ik hier Piet en Hans bedanken, die naast de talrijke staalnames ook serieus wat werk in het lab (meten, determineren, analyseren, informatiseren) verricht hebben. Menig keer hebben we er het boek bijgehaald (al dan niet met een stevig Belgisch biertje in de hand), om te zien of er nu wel of niet een vlekje of een stekeltje meer of minder te zien of te voelen was.

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Een doctoraat komt zelden op zijn eentje tot stand. *Louise Puturuhu*, *Mattias Verbeke*, *Peter Sas*, *Dries van Toortelboom*, *Katrien De Merlier*, *Katrijn Deroose*, *Robby Herfs* en *Gaëtan Verschraege*, hebben via thesissen en maandwerken een deel van het maaganalyse werk verricht.

In totaal werden er voor dit doctoraat 3560 boomkorstalen genomen in het Nederlandse Delta gebied, waarvan 2350 door de sectie Mariene Biologie. Ikzelf was vanaf 1990 iets meer dan 100 dagen op 'zee' voor mijn doctoraat. En het mag gezegd: het was dikwijls mooi weer, maar ook regen, wind en kou hebben we getrotseerd. Daarom wil ik alle mensen bedanken die mee waren op de verschillende staalnames of die geholpen hebben in het lab. Meer bepaald *Johan van de Velde*, *Bernard Timmerman*, *Annick Van Kenhove*, *Danielle Schram*, *Guy De Smet en Dirk Van Gansbeke*, en natuurlijk alle anderen (veel te veel om op te noemen) die

vroeg of laat wel eens ingesprongen zijn, ook diegenen vanuit het CEME, de KULeuven of 'den privé'. In het bijzonder *Gonda Geets*, *Renato Arellano* en *Ben de Bree*, met wie ik toch serieus wat uren op 'den boot' heb doorgebracht: 'ge zid ool zê-kapietings van t'jest'eure'.

Sowieso alle collega's van de sektie Mariene Biologie ('t komt ervan aje gekend zît lik vorte vis), maar meer bepaald een paar (ex-)collega's van *Goby Systems Unlimited,* wil ik eveneens bedanken voor de werksfeer, de discussies, vriendschap, staalnames, en zowat alles wat we samen gedeeld hebben. *André Cattrijsse*, *Jan Mees*, *Bregje Beyst* en *Ann Dewicke* hebben ondertussen het nest verlaten, maar *Nancy Fockedey*, *Henriet-ta Hampel* en alle anderen blijven het hyperbenthos en visonderzoek hoog houden. Ook *Natascha Chavatte*: de babbels om jou er weer tegenaan te laten gaan, hebben mij het laatste jaar en de laatste weken evenveel deugd gedaan. In het bijzonder moet ik hier ook *Olivier Hamerlynck, bezieler van Goby Systems* vernoemen. Hij bracht me de 'eerste en vergevorderde beginselen der vissen-ecologie' bij, en hielp me bij het opstarten van dit doctoraat, getuige de diverse artikels die we samen publiceerden. Nu de doctorstitel niet meer ver-af is, kan ik misschien eindelijk mijn 'Arctic Dreams' gaan najagen.

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I would like to thank all people who were involved in the FAIR concerted action, a difficult task to bring together all existing information on fishes in estuaries, but which finally delivered a splendid and useful book. I ample used it as a source for the present thesis. In other words: a fruitful cooperation, susceptible for repetition.

Aan alle vrienden/vriendinnen CWC-ers, Tjoolaers en Ordessanen/Mercantourianen: chaos was er meestal wel, 'getjoold' heb ik meer dan een beetje (niet in het minst gedurende de laatste maanden) en afzien bij het klimmen naar de eindmeet heeft zo zijn sporen nagelaten. Het *vogelen* en *wandelen* waren aangename afwisselingen met het *zitten* achter een laptop. En zie, 'oles komt ûteindlik up zîn pwoitjes nere'. Kunnen we eindelijk eens praten over de inhoud i.p.v. de deadline (die toch wel een paar keer verschoven is ☺).

Mijn vader zal het niet meemaken, en mijn stiefvader helaas ook niet meer. Mijn *moeder* heeft me desondanks en met alle moeilijkheden van dien 'mijn gang laten gaan'. Dit doctoraat is dan ook ten volle aan haar opgedragen. Mijn broers, zussen, schoonbroer en hun *entourage* (jullie zijn ondertussen met z'n zevenentwintigen, veel te veel om hier allemaal te vernoemen) hebben in dit alles ook wel op de één of andere manier de nodige bijdrage en ondersteuning gegeven. Ik heb jullie lang genoeg laten wachten: ten zeerste bedankt. Ook mijn *schoonouders* wil ik hier speciaal bedanken voor alle steun en opvang, niet in het minst de voorbije maand bij het leggen van de laatste loodjes (ze wegen inderdaad echt wel het zwaarst).

En dan natuurlijk *Els*, het laatste jaar en vooral de laatste maanden heeft ze het volledige gezin (*Sam*, *Lars* en mezelf inclusief) op haar schouders gedragen, en tussendoor ook nog voor de nodige ontspanning gezorgd. What's a man without a woman? Ik zou zeggen: 'ne welgemjênde 'kzie joe geirn'. Het ei is gelegd, een mooier verjaardagscadeau kon ik je (zij het met enige vertraging) waarschijnlijk niet geven. Ook de 'kids' *Sam* en *Lars* ten zeerste bedankt, jullie hebben mij de laatste maanden lang genoeg moeten missen, en al-hoewel jullie maar half (of helemaal niet) beseffen wat er aan de hand is, de 'kiekeboes', de 'huppakees', de 'lachsalvos', enz. hebben er meerdere keren voor gezorgd dat ik de tijd achter dit beeldscherm heb over-leefd. Straks eindelijk weer tijd om samen met de hele kroost eens op een andere manier te gaan 'booje vawe'.

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Mogelijks zal ik wel iemand vergeten zijn te bedanken. Ik zou zeggen: 'iermee zie'je wok bedankt'. Veel lees-genot, of om het met de woorden van *Luc de Vos* te zeggen: "Lieve kleine piranha, verscheur mij!"

24 januari 2003

Kris

TABLE OF CONTENTS

SUMMARY

The present thesis focuses on the role of the Westerschelde and Oosterschelde estuaries (Southern Bight of the North Sea) as nursery areas for demersal fish and macro-invertebrate species. The main aim of the thesis is to provide a baseline about the higher trophic levels for future process studies in the Delta area. The nursery function depends on recruitment of (post)larvae into the system, habitat complexity and availability, environmental properties and prey availability. The environmental/biological and biological/biological interactions act both as extrinsic and intrinsic forcing variables on the structure of the demersal fish and macro-invertebrate assemblages.

The five main **objectives** of the thesis were: (1) to describe the structural patterns in species composition, diversity, density, biomass and growth in the assemblages in relation to the environmental characteristics of both estuaries; (2) to describe these patterns at several temporal (short-, mid- and long-term changes) and spatial scales (within and between estuaries and subhabitats); (3) to evaluate both abiotic and biotic influences at the community level, and to predict distribution patterns at the species level; (4) to investigate temporal and spatial differences in trophic niche and feeding patterns of several fish and macro-invertebrate species in the Westerschelde estuary; and (5) to evaluate the importance of hyperbenthic organisms, and in particular mysids, in the food web of the Westerschelde estuary.

The introduction to the thesis (**Chapter 1**) starts with a general description of the epibenthic assemblages and a short overview of the factors on which the nursery function of a system depends. Then follows a description of the study area, the different sampling methodologies, the available data sets, and the general outline of the thesis.

The Westerschelde and Oosterschelde estuaries are located within the Dutch Delta area (SW Netherlands). The Westerschelde estuary is affected by high organic waste loads and by industrial pollution. The Oosterschelde has been altered into a marine bay, through major engineering works during the past decades.

Different sampling methodologies have been used: a 3-m beam trawl in the subtidal of both estuaries, a 2-m beam trawl on the intertidal flats of the Westerschelde, fyke nets on the intertidal flats of the Oosterschelde, a stow net in the intertidal saltmarsh creeks of the Westerschelde, and a hyperbenthic sledge in the subtidal Westerschelde. The latter gear mainly sampled larval and early post-larval fish and macro-crustaceans. The thesis benefits from the research on other biotic compartments, especially on the subtidal hyperbenthos and the nekton fauna in the saltmarsh creeks.

Long-term monitoring in a more or less uniform way has produced a large amount of data on the ecology of the demersal fish and macro-invertebrate fauna in the Dutch Delta area, and in the Westerschelde and Oosterschelde estuary in particular, covering two decades from 1983 through 2001, but with a gap in 1993-'98. Such a thorough baseline study is a prerequisite for monitoring the impact assessment of possible environmental changes in these systems in the future.

The spatial and temporal **structural** patterns in the fish and macro-invertebrate assemblages, are described in **PART I** (chapters 2 through 6, supplemented with five addenda). These were mainly based on subtidal data gathered with a 3-m beam trawl in both estuaries. The addenda are merely given for completeness, as they contain complementary information to both estuaries, mainly from the ebb-tidal Voordelta area.

In **Chapter 2**, the spatial and short-term temporal patterns along the salinity gradient in the subtidal Westerschelde are described, based on monthly data of the period 1988-'89, and in an **addendum** of 1990. In a **second addendum** the usefulness of multivariate techniques is demonstrated, based on subtidal data from the Westerschelde in combination with data from neighbouring areas, like the Oosterschelde and the Voordelta.

At the end of the 1980s, the Westerschelde estuary harboured high densities of demersal fish and macro-crustaceans. Only 37 fish species were recorded and 3 mobile macro-invertebrate species were quantified. The near absence of anadromous and freshwater species was correlated with the low oxygen concentrations upstream the Dutch-Belgian border.

Seventeen species were common, only eight of which were really abundant. An overall dominance of the brown shrimp *Crangon crangon* was

noted. The demersal fish and macro-crustacean assemblage could be divided into a marine and a brackish community along the main salinity-oxygen-turbidity gradients of the estuary. Higher densities and biomasses for brown shrimp, several gobies and several flatfish species were recorded in the brackish part. The spatial structure in the marine assemblage seemed to be influenced by the water masses from the sea and inflowing channels, and was correlated with the degree of exposure (current velocities and tides).

Also, the comparative study between the three ecosystems in the Dutch Delta area, proved that quite accurate predictions of the expected community types could be made, given a fairly limited number of environmental variables, mainly salinity, and exposure/substratum type. Rich and varied communities were found in the ebb-tidal deltas of the Oosterschelde and the Grevelingen, an impoverished fauna in the Westerschelde, and density-poor but species-rich communities in the Oosterschelde.

The use of ecological guilds has been widely accepted to describe common patterns of estuarine usage. Additionally, a classification is proposed, based on the seasons in which the species occur in the Westerschelde estuary, and on their life stages and abundances during that period. The monthly data demonstrated that while the eight abundant species were generally present throughout the year (summer- or winter-resident), the majority tended to appear in the Westerschelde at varying times (summer, winter or bimodal) and often remained in large numbers (nine common species) for only a short time.

In **Chapter 3,** spatial and mid-term patterns in the fish assemblages of the Oosterschelde are presented, based on subtidal fortnightly samples in 1988 (in comparison to the Westerschelde and Voordelta) and on quarterly samples in the period 1988-'89 (in comparison to the period 1984-'85). Also, in an **addendum** based on intertidal data gathered with fykes and a weir between 1979-'88, we tried to evaluate the mid-term responses of the fish fauna to the construction of the storm-surge barrier in the mouth and the compartmentalization dams at the landward side.

Diversity was higher in the Oosterschelde than in the Voordelta or the Westerschelde. Annual production of the fish and macro-invertebrate assemblages in the Oosterschelde was estimated at about 6 gADW m^{-2} yr^{-1}, annual consumption was estimated at over 25 gADW m^{-2} yr^{-1}. However, these results were highly dependent on the assumptions. Over 85 % of the Oosterschelde production was accounted for by only six species: starfish *Asterias rubens*, plaice *Pleuronectes platessa*, bib *Trisopterus luscus*, brown shrimp *Crangon crangon*, shore crab *Carcinus maenas* and dab *Limanda limanda*. In spite of its abundance, the sand goby *Pomatoschistus minutus* contributed little to the annual production.

Multivariate statistical techniques revealed four communities in the Oosterschelde, the most seaward communities being the richest. From the available data, it was difficult to assess the impact of these major engineering works on the demersal fish and macro-invertebrate fauna. The increase in flatfish in the western part is probably linked to a local decrease in current velocities. On the other hand, the increase in the gadoids bib *Trisopterus luscus* and whiting *Merlangius merlangus* was predominated by stronger year-classes in the post-barrier time period. Lower nutrient inputs through the northern part, in combination with the increase in gadoid densities, may have resulted in a decline in the brown shrimp *Crangon crangon* in the Oosterschelde. Also, several other species showed a decreased trend at the end of the 1980s.

Based on the annual averages in frequency of occurrence, the intertidal fish community from the period 1979-'84 was separated from the period 1985-'88. Comparable with the results from the subtidal beam trawl catches, many of the changes were related to fluctuations in year-class strength, or to changes on a wider geographical scale. Only the decrease in anadromous fish in the Oosterschelde could be attributed to the engineering works, as the fresh water connections were dammed.

In **Chapter 4,** long-term patterns in the fish fauna of the Oosterschelde are presented, based on quarterly data from the periods 1987-'89 and 1999-2001. This chapter deals with the possible effects a decade after completion of the Delta-works in the Oosterschelde. In an **addendum**, the consequences of the civil engineering works in the ebb-tidal deltas of the Grevelingen and Oosterschelde are evaluated.

In comparison to the period 1987-'89, on average 6 more (mainly occasional) species were recorded per season in the period 1999-2001, with a total of 42 fish species in the latter period. This was comparable to the period 1960-'76, although diadromous species (*e.g.* smelt *Osmerus eperlanus* and eel *Anguilla anguilla*) showed a reduced frequency of occurrence. The commonest species in both periods were sand goby *Pomatoschistus minutus*, plaice *Pleuronectes platessa*, dab *Limanda limanda* and bib *Trisopterus luscus*.

Multivariate analyses revealed seasonal differences (autumn-winter *versus* spring-summer), with a separation of the period 1987-'89 from 1999-2001. Highest densities of the estuarine resident and marine juvenile species (0- and 1+ group individuals) were recorded in summer and autumn. A 45 % increase in total average fish density was noted in 1999-2001, mainly attributed to *Pomatoschistus minutus*, while the total average biomass decreased with 35 %. For most species, the long-term differences in density and biomass were not directly due to the engineering works in the Oosterschelde. Either they reflected

natural population variability due to a delayed appearance of strong year-classes after cold winters (*e.g.* high densities of *Pleuronectes platessa* and *Limanda limanda* in 1987), or changes were obscured through sampling bias (*e.g.* an increased net-efficiency through clogging of the nets for nilsson's pipefish *Syngnathus rostellatus* and *Pomatoschistus minutus* in 1999-2001, or an unexplained reduced efficiency for gobies in 1987-'89).

Also, spatial differences were found in both periods, with highest densities (10 species) in the western and northern parts, increased densities (28 species) in the central part, and decreased densities (16 species) in the eastern part of the Oosterschelde estuary. A correlation between high species densities and substratum type (>50 % silt concentration, mainly in the western and northern parts) was observed. Still, for most species the loss at one station was compensated with an increase at another station in most subareas. This may be related to local changes in food resources (e.g. blue mussel *Mytilus edulis* for flatfish in the western part, brown shrimp *Crangon crangon* for dragonet *Callionymus lyra* in the central part, and high macro- and hyperbenthic biomasses in the northern part).

Estuarine ecosystems like the Oosterschelde are able to absorb and adjust to changes, but they can also be very vulnerable. In the Voordelta area, much higher densities for several benthic organisms (fish, macro-invertebrates, macrobenthos and hyperbenthos) were recorded in the ebb-tidal delta of the Grevelingen in the period 1988-'89, as compared to the ebb-tidal delta of the Oosterschelde. The increased importance for flatfish, especially dab *Limanda limanda* and sole *Solea solea*, was probably related to changed hydrodynamics since the closure of the Grevelingen estuary in 1971, where the ebb-tidal delta of the Grevelingen acts as a trap and retains mud, detritus, eggs and larvae. However, the increased nursery function of the ebb-tidal delta does not make up for the loss of nursery areas in the estuary itself.

In the previous chapters only the most conspicuous (and abundant) macro-invertebrate species were taken into account. In **Chapter 5**, detailed short- and long-term patterns for several macro-invertebrates are given, in a comparison between the Westerschelde and Oosterschelde estuaries, based on quarterly data from the periods 1988-'89 and 1999-2001. Higher densities in the latter period were correlated with mild winters, abundance of food resources, engineering works, and presence of intertidal habitat.

Diversity patterns were influenced by salinity, sediment/habitat type, temperature, and the introduction of alien species (mainly crabs). In the Oosterschelde, 33 macro-invertebrate species were recorded in the period 1999-2001: 9 caridean prawns, 9 brachyuran crabs, 6 echinoderms, 3 caridean shrimps, 3 cephalopods, 2 anomuran crabs and 1 lobster. The dominating species in the Oosterschelde were brittlestar *Ophiura* species, brown shrimp *Crangon crangon*, starfish *Asterias rubens*, shore crab *Carcinus maenas* and hermit crab *Pagurus bernhardus*. Diversity in the Westerschelde was much lower, with only 8 species recorded: 4 brachyuran crabs, 2 caridean prawns, 1 caridean shrimp, and 1 anomuran crab, and an overall dominance of *Crangon crangon*.

Seasonal distribution patterns in macro-invertebrate densities in both estuaries were related to annual changes in temperature and dissolved oxygen concentration. A number of species stayed for a short period (with highest densities in the warmer seasons), while others were present in considerable densities throughout the year.

Different spatial patterns in species composition were only found between the marine and brackish part in the Westerschelde, related to the salinity-turbidity gradients. The (re-)occurrence of the caridean prawn *Palaemon longirostris* in the Westerschelde possibly reflects an improved water quality.

In **Chapter 6**, we try to predict the occurrence and abundance of 12 fish and 3 macro-crustacean species, through a limited set of environmental variables (temperature, salinity, dissolved oxygen concentration and turbidity, and/or their quadratic effects) in the Westerschelde. Most data from the subtidal surveys (1988-'91 and 1999-2001) are used. In an **addendum**, these models are applied to a dataset from the Oosterschelde.

The maximum likelihood of occurrence could be predicted fairly well in both estuaries, by means of single-species (multiple) logistic regression models. Sensitivity (% present predicted as present) and specificity (% absent predicted as absent) were equally high in most models, and validation proved the models to be accurate and robust. The combined interaction of the different environmental variables was more powerful to predict species occurrence than every single variable, where the seasonal patterns dominated over the spatial patterns. The addition of other variables (current velocity, mysid prey density, chlorophyll a or suspended particulate matter) did not improve the predictions.

Prediction of single species abundance by means of multiple linear regressions, constrained by the same characterizing variables was partly successful. Probably, other variables are needed to improve the prediction of density, and to highlight the underlying causal relationships. Best models were built for seven species that were present in the estuary for a longer period, but with only one clear density peak, *i.e.* dab *Limanda limanda*, common goby *Pomatoschistus microps*, shore crab *Carcinus maenas*, flying crab *Liocarcinus holsatus*, flounder *Platichthys flesus*, sprat *Sprattus sprattus* and sand goby *Pomato-*

schistus minutus. Densities of these species were structured mainly by the environmental patterns. Applicability of these best-fitting models to the Oosterschelde was limited, as no spatial gradient in salinity exists in this ecosystem, and a number of species showed different distribution patterns in both estuaries.

Models with a low predictive value were constructed for eight species that only stayed for a short period (*i.e.* bib *Trisopterus luscus*, whiting *Merlangius merlangus* and nilsson's pipefish *Syngnathus rostellatus*) or that showed two density peaks (*i.e.* herring *Clupea harengus*, sole *Solea solea*, plaice *Pleuronectes platessa*, brown shrimp *Crangon crangon*, and lozano's goby *Pomatoschistus lozanoi*). Densities of these species were probably mainly correlated with prey availability.

In **PART II**, the **functioning** of the different habitats in the Westerschelde as nurseries for juvenile fish and macro-crustaceans, and the role of hyperbenthic prey – and of mysids in particular – for the higher trophic levels of the estuarine food web, are evaluated. Data from different sub- and intertidal beam trawl surveys were used in chapters 7 and 8 (supplemented with 2 addenda).

In **Chapter 7**, the diet of 25 fish species in the Westerschelde is investigated through *ca.* 1500 stomach content analyses. A paper on the feeding ecology of two gadoid species in the Voordelta is given as **addendum**.

A number of species, like sand goby *Pomatoschistus minutus* and bib *Trisopterus luscus* showed diet shifts from calanoid copepods to mysids. Also in the Voordelta, *T. luscus* and whiting *Merlangius merlangus* changed from copepods over mysids to shrimp and fish with increasing size. Both ontogenetic and seasonal shifts in the diet were related with growth of the species and prey availability. Total annual consumption of both gadoid species together in the Voordelta was estimated at 0.47 – 0.57 g ADW m^{-2} yr^{-1}.

In the subtidal food webs of the Westerschelde (see Chapter 9), the major energy flow between the secondary trophic level and the demersal fish and macro-crustaceans, mainly passes through the 'pelagic' food-chain. Small crustaceans (copepods, mysids, amphipods) constituted the main diet component, with an overall dominance of mysids. Most of the prey species (including species that are normally endobenthic or zooplanktonic) were found to be common organisms in the hyperbenthic water layer. Furtheron, a different foraging strategy was shown for two flatfish species (plaice *Pleuronectes platessa* and flounder *Platichthys flesus*), which mainly foraged in the intertidal, on amphipods, bivalves and polychaetes. Next to a typical subtidal foraging behaviour, several fish species and brown shrimp *Crangon crangon* (see Chapter 8) also foraged in the intertidal, mainly on amphipods.

Mysidacea occurred in >50 % stomachs analysed and were taken as prey by 19 of the 25 fish species. Mysids were most important in the diets of *T. luscus*, *M. merlangius*, *P. minutus* and lozano's goby *Pomatoschistus lozanoi*, and were present in appreciable numbers in *P. flesus*, tub gurnard *Trigla lucerna*, herring *Clupea harengus* and *P. platessa*. These species mainly fed on the brackish water endemic *Neomysis integer*, while *Mesopodopsis slabberi* (present in 35 % of the gobiid stomachs) and *Gastrosaccus spinifer* (present in 25 % of the gadoid stomachs) were of secondary importance. It was estimated that only 1 % of the standing stocks of the mysid populations was removed per day by the local demersal fish assemblage.

In **Chapter 8**, diurnal, seasonal and spatial patterns in the diet of the brown shrimp *Crangon crangon* in the Westerschelde are presented, based on two 24-h surveys in September 1991 in the brackish subtidal, seasonal samples in the marine and brackish subtidal in the period 1999-2000, and monthly intertidal samples in 1992. In an **addendum**, a basic paper on the food webs of the Westerschelde is included.

Of all stomachs examined, 36 % were empty, 33 % had few (highly digested) remains (mainly from crustaceans), and 31 % contained many (partly digested) prey items. Minimum and maximum daily consumption values amounted to 1-5 % bodyweight per day in the subtidal, and 4-14 % BW d^{-1} intertidally. Yearly consumption was 1-8 gADW m^{-2} yr^{-1}, both sub- and intertidally.

On a daily scale, density, feeding intensity and prey diversity showed mixed tidal-diurnal patterns, with the tidal effect dominating over the diurnal effect. More feeding and a higher trophic diversity were found at high water. Mysids (mainly *Neomysis integer* and *Mesopodopsis slabberi*) were the most important prey items, both during the day and at night. It is suggested that *C. crangon* mainly forages in the hyperbenthic waterlayer at night, and supplements its diet with some prey taken from the epibenthic layer during the day.

On a seasonal scale, density and prey diversity were highest during summer, both sub- and intertidally. The tidal influence partly masked the seasonal variation in stomach fullness. Although different food webs are known to exist in the marine and brackish part of the Westerschelde, this is not really reflected in the higher trophic levels. Mysids were important prey items in spring and summer in the subtidal throughout the estuary. Only the species changed: mainly *Gastrosaccus spinifer* in the marine part, and *N. integer* and *M. slabberi* in the brackish part. In the brackish zone, mysids were replaced by amphipods (*Corophium* and *Bathyporeia* species) in

autumn and winter, which paralleled the seasonal patterns in prey abundance and prey availability.

On a spatial scale, prey diversity was higher in the brackish intertidal than in the subtidal, but mysids were infrequently preyed upon intertidally. In this subhabitat, copepods were gradually replaced by amphipods (*Corophium*) in the diet, with increasing size of *C. crangon*.

Shrimp predation impact on the mysid populations is much larger than that of the fish assemblage: on average 10 to 35 % of the mysid standing stocks was consumed per day by *C. crangon*.

Finally, in **Chapter 9**, an overview is given on the nursery function of the Westerschelde and Oosterschelde estuaries for demersal fish and macro-invertebrates, based on all data sets presented in this thesis, including a link between (post)larval and juvenile appearance in the subtidal of both estuaries, and in several subhabitats in the Westerschelde estuary.

Larvae and early-postlarvae of 17 fish and 11 macro-crustaceans were recorded, in the Westerschelde and/or Oosterschelde, mainly in spring and in the intertidal salt marsh creeks. A clear seasonal succession of different life history stages (postlarva – juvenile – immature - adult) of different species in different subhabitats (intertidal marsh creeks - intertidal flats - subtidal) has been shown.

Biodiversity is related to habitat use and habitat availability. In total 96 fish species have been recorded during the last two decades in all subhabitats, 75 species in the Oosterschelde and 74 in the Schelde estuary (including the tidal zone upstream of the Westerschelde).

The present thesis provides a baseline on the fish and macro-invertebrate assemblages in the Westerschelde and Oosterschelde. The thesis suggests that both estuaries play a significant role as nursery areas for several demersal fish and macro-invertebrate species. The analysis of the structure and functioning of the demersal fish and macro-invertebrate assemblages in the Westerschelde and Oosterschelde estuaries, at several spatial and temporal scales has yielded 10 major conclusions, which are presented throughout the different chapters of the thesis. Finally, some remarks on the thesis and some recommendations for future research are given.

SAMENVATTING

In dit proefschrift wordt de rol van de Westerschelde en de Oosterschelde estuaria (Zuidelijke Bocht van de Noordzee) als opgroeigebieden voor demersale vissen en macro-invertebraten onderzocht. Het proefschrift heeft als belangrijke doelstelling een sterke basis te vormen wat betreft de hogere trofische niveaus naar toekomstige proces-studies in het Delta gebied. De kinderkamerfunctie van estuaria is afhankelijk van de rekrutering van (post)larven in het systeem, van de complexiteit en beschikbaarheid van geschikte habitats, van de omgevingskarakteristieken, en van de beschikbaarheid van prooiorganismen. De interacties tussen de soorten onderling en tussen de soorten en de omgeving, oefenen zowel een intrinsieke als extrinsieke invloed uit op de structuur van de demersale vis- en macro-invertebraten gemeenschappen.

Vijf doelstellingen staan centraal: (1) het beschrijven van de structurele patronen in soortensamenstelling, diversiteit, densiteit, biomassa en groei in de gemeenschappen, dit in relatie tot de omgevingskarakteristieken in beide estuaria; (2) het beschrijven van deze patronen op verschillende temporele (veranderingen op korte, middellange en lange termijn) en ruimtelijke schalen (binnenin en tussen estuaria en subhabitats); (3) het evalueren van de abiotische en biotische invloeden op het niveau van de gemeenschappen, en het voorspellen van de verspreidingspatronen op soortniveau; (4) het onderzoeken van de temporele en ruimtelijke verschillen in de trofische niche en in de voedingspatronen van verschillende soorten vissen en macro-invertebraten in de Westerschelde; en (5) het evalueren van het belang van hyperbenthische organismen- in het bijzonder aasgarnalen - in het voedselweb van het Westerschelde estuarium.

De inleiding tot het proefschrift (**Hoofdstuk 1**) begint met een algemene beschrijving van de demersale vis- en macro-invertebraten gemeenschappen en een kort overzicht van de factoren waarvan de kinderkamerfunctie afhankelijk is. Dan volgt een beschrijving van het studiegebied, de verschillende bemonsteringstechnieken, de beschikbare datasets en de algemene omkadering en structuur van het proefschrift.

De Westerschelde en Oosterschelde estuaria vormen een deel van het Nederlandse Deltagebied (ZW Nederland). De Westerschelde is onderhevig aan een hoge organische belasting afkomstig van ongezuiverd rioolwater en aan industriële vervuiling. De Oosterschelde werd omgevormd van een estuarium naar een mariene baai d.m.v. een aantal grote waterbouwkundige ingrepen tijdens de laatste decennia.

Verschillende bemonsteringstechnieken werden gebruikt: een 3-m boomkor in het subtidaal (de diepere delen) van beide estuaria, een 2-m boomkor op de intertidale zandplaten (intergetijdengebied) in de Westerschelde, fuiknetten op de intertidale platen in de Oosterschelde, een staand net in de intertidale schorkreken in het brakwater gedeelte van de Westerschelde, en een hyperbenthische slee in het subtidaal van de Westerschelde. Deze laatste techniek was vooral gericht op het bemonsteren van larvale en vroeg post-larvale vissen en macro-invertebraten. De thesis maakt gebruik van het onderzoek verricht naar andere biotische componenten, in het bijzonder de studies over het subtidale hyperbenthos en de nekton fauna in schorkreken.

Lange-termijn monitoring - gespreid over twee decennia van 1983 t.e.m. 2001, maar met een leemte in de periode 1993-'98 - heeft een grote hoeveelheid aan gegevens opgeleverd over de ecologie van de demersale vis- en macro-invertebraten fauna in het Nederlandse Delta gebied in het algemeen, en in de Westerschelde en Oosterschelde estuaria in het bijzonder. Een dergelijk uitgebreid basisonderzoek is een eerste vereiste voor het maken van impactstudies naar mogelijke toekomstige veranderingen in de omgeving.

De ruimtelijke en temporele structurele patronen in de vis- en macro-invertebraten gemeenschappen worden beschreven in **DEEL I** (Hoofdstukken 2 t.e.m. 6, aangevuld met 5 addenda). Deze zijn voornamelijk gebaseerd op subtidale gegevens, verzameld met een 3-m boomkor in beide estuaria. De addenda dienen vooral tot vervollediging van het proefschrift met complementaire informatie over het Voordelta gebied.

In **Hoofdstuk 2** werden de ruimtelijke patronen langsheen de saliniteitsgradiënt en de temporele patronen op korte termijn beschreven voor het subtidale

gebied in de Westerschelde, gebaseerd op maandelijkse gegevens van de periode 1988-'89, en in een **addendum** voor 1990. In een **tweede addendum** wordt het nut van multivariate technieken aangetoond, gebaseerd op subtidale gegevens van de Westerschelde in combinatie met gegevens van aangrenzende gebieden, zoals de Oosterschelde en de Voordelta.

Op het einde van de 1980-er jaren werden hoge densiteiten aan demersale vissen en macrocrustaceeën genoteerd in het Westerschelde estuarium. Slechts 37 vissoorten werden gevangen en 3 soorten macro-invertebraten werden gekwantificeerd. Anadrome en zoetwater soorten waren zo goed als afwezig. Dit was gecorreleerd met de lage concentraties opgeloste zuurstof stroomopwaarts van de Belgisch-Nederlandse grens.

Zeventien soorten waren algemeen, en slechts acht soorten waren overvloedig aanwezig, met een algemene dominantie van de grijze garnaal *Crangon crangon*. De demersale vis- en macrocrustaceeën gemeenschap kon worden opgedeeld in een mariene en een brakwatergemeenschap langsheen de belangrijkste gradiënten in saliniteit-zuurstof-troebelheid in het estuarium. Hogere densiteiten en biomassa's aan grijze garnaal, verschillende grondelsoorten en verschillende soorten platvis werden genoteerd in het brakwatergedeelte. De ruimtelijke structuur in de marine gemeenschap werd waarschijnlijk beïnvloed door de watermassa's van de zee en de toevoerkanalen, en was gecorreleerd met de hydrodynamische condities (stroomsnelheden en getijden).

Ook de vergelijkende studie tussen de drie ecosystemen in het Nederlandse Deltagebied toonde aan dat op basis van slechts enkele omgevingsvariabelen (voornamelijk saliniteit en graad van blootstelling/substraat type) vrij accurate voorspellingen van de te verwachten gemeenschappen kunnen worden gemaakt.,. Rijke en diverse gemeenschappen waren aanwezig in de buitendelta's van de Oosterschelde en de Grevelingen, een verarmde fauna in de Westerschelde, en soortenrijke gemeenschappen met een lage densiteit in de Oosterschelde.

Het concept van ecologische groepen ('guilds') wordt algemeen aanvaard om gemeenschappelijke patronen in het gebruik van estuaria te beschrijven. Aanvullend werd een classificatie voorgesteld, gebaseerd op de seizoenen waarin de soorten voorkomen in de Westerschelde en op de verschillende levensstadia en densiteiten gedurende die periode. De maandelijkse gegevens tonen aan dat, alhoewel de acht meest abundante soorten gewoonlijk aanwezig zijn gedurende het ganse jaar (zomer- of winter-residenten), de meerderheid van de soorten eerder op specifieke tijdstippen en gedurende een korte periode voorkomt in de Westerschelde (zomer-, winter- of bimodale soorten) en dan dikwijls in hoge aantallen (negen algemene soorten).

In **Hoofdstuk 3** worden de ruimtelijke patronen en de patronen op middellange termijn in de subtidale visgemeenschappen van de Oosterschelde voorgesteld, gebaseerd op veertiendaagse bemonsteringen in 1988 (voor een vergelijking met de Westerschelde en de Voordelta) en op kwartaalbemonsteringen in de periode 1988-'89 (voor een vergelijking met de periode 1984-'85). In een **addendum**, gebaseerd op intertidale gegevens verzameld met fuiken en een keernet in de periode 1979-'88, wordt de respons van de visfauna op de constructie van de stormvloedkering in de monding en de compartimentalisatie-dammen landinwaarts onderzocht.

De diversiteit was hoger in de Oosterschelde dan in de Voordelta en de Westerschelde. De jaarlijkse productie van de vis- en macro-invertebraten gemeenschappen in de Oosterschelde werd geschat op 6 gADW m^{-2} jr^{-1}, de jaarlijkse consumptie werd geschat op 25 gADW m^{-2} jr^{-1}. Meer dan 85 % van de productie in de Oosterschelde werd toegeschreven aan slechts zes soorten: zeester *Asterias rubens*, schol *Pleuronectes platessa*, steenbolk *Trisopterus luscus*, grijze garnaal *Crangon crangon*, strandkrab *Carcinus maenas* en schar *Limanda limanda*. Ondanks de hoge densiteiten was de bijdrage van dikkopje *Pomatoschistus minutus* tot de jaarlijkse productie zeer beperkt.

Multivariate statistische technieken onderscheidden vier gemeenschappen in de Oosterschelde, waarbij de meest zeewaarts gelegen gemeenschappen het rijkst waren. Met de beschikbare gegevens was het moeilijk om de impact van de waterbouwkundige werken op de demersale vis- en macro-invertebraten fauna te beoordelen. De toename in platvis densiteiten in het westelijk gedeelte was waarschijnlijk gerelateerd met een locale afname van de stroomsnelheden. Aan de andere kant werd de toename aan kabeljauwachtigen (steenbolk *Trisopterus luscus* en wijting *Merlangius merlangus*) overheerst door sterke jaarklassen in de "post-kering" periode. Een verminderde aanvoer van nutriënten doorheen het noordelijke gedeelte, in combinatie met een toename aan kabeljauwachtigen, zou aan de basis kunnen liggen van de afname aan grijze garnaal *Crangon crangon* in de Oosterschelde. Ook andere soorten vertoonden een dalende trend aan het eind van de jaren tachtig.

Gebaseerd op de jaarlijkse gemiddelde frequentie van voorkomen, kon de intertidale visgemeenschap van de periode 1979-'84 onderscheiden worden van deze van de periode 1985-'88. Naar analogie met de resultaten van de boomkor staalnames in het subtidaal, konden de meeste veranderingen toegeschreven worden aan fluctuaties in jaarklasse-sterkte of aan veranderingen op een grotere geografische schaal. Alleen de afname van anadrome vissen in de Oosterschelde kon worden toegeschreven aan de waterbouwkundige werken, doordat de zoetwater inlaten werden afgedamd.

In **Hoofdstuk 4** worden de lange-termijn patronen in de visfauna van de Oosterschelde weergegeven, gebaseerd op kwartaalgegevens van de periodes 1987-'89 en 1999-2001. Dit hoofdstuk handelt over de mogelijke effecten van de Delta-werken in de Oosterschelde een decennium na de voltooiing. In een **addendum** worden de gevolgen van waterbouwkundige werken in de buitendelta's van de Grevelingen en de Oosterschelde geëvalueerd.

In vergelijking met de periode 1987-'89 werden per seizoen gemiddeld 6 (vooral occasionele) soorten meer gevonden in de periode 1999-2001, met een totaal van 42 vissoorten in deze laatste periode. Dit was vergelijkbaar met de periode 1960-'76, alhoewel de frequentie van voorkomen van de diadrome soorten (*vb.* spiering *Osmerus eperlanus* en paling *Anguilla anguilla*) was verminderd. De algemeenste soorten in beide periodes waren dikkopje *Pomatoschistus minutus*, schol *Pleuronectes platessa*, schar *Limanda limanda* en steenbolk *Trisopterus luscus*.

Multivariate analyses toonden seizoenale verschillen aan (herfst-winter *versus* lente-zomer), en een scheiding tussen de periodes 1987-'89 en 1999-2001. De hoogste densiteiten aan estuariene residente en mariene juveniele soorten (0- en 1+ individuen) werden genoteerd in de zomer en de herfst. De totale gemiddelde densiteit aan vis was met 45 % toegenomen in 1999-2001, vooral te wijten aan *P. minutus*, terwijl de totale gemiddelde biomassa was afgenomen met 35 %. Voor de meeste soorten konden de lange-termijn verschillen in densiteit en biomassa niet direct gerelateerd worden aan de Delta-werken. Ofwel waren het weerspiegelingen van een natuurlijke populatie variabiliteit te wijten aan het vertraagd verschijnen van sterke jaarklassen na koude winters (*vb.* hoge densiteiten aan *P. platessa* en *L. limanda* in 1987), ofwel werden de veranderingen verdoezeld door onnauwkeurigheden tijdens de staalnames (*vb.* een verhoogde net-efficiëntie door verstopping van de mazen voor kleine zeenaald *Syngnathus rostellatus* en *P. minutus* in 1999-2001, of een verminderde net-efficiëntie voor grondels in 1987-'89 die niet kon worden verklaard).

Ook ruimtelijke verschillen werden aangetoond in beide periodes, met hoogste densiteiten (voor 10 soorten) in de westelijke en noordelijke delen, toegenomen densiteiten (voor 28 soorten) in het centrale deel en afgenomen densiteiten (voor 16 soorten) in het oostelijk deel van de Oosterschelde. Hoge densiteiten waren gecorreleerd met substraat type (>50 % slib, vooral in de westelijke en noordelijke delen). Nochtans werd voor de meeste soorten het verlies in het ene station gecompenseerd met een stijging in een ander station. Dit kan gerelateerd zijn aan locale veranderingen in voedselbronnen (vb. mossel *Mytilus edulis* voor platvis in het westelijk deel, grijze garnaal *C. crangon* voor pitvis *Callionymus lyra* in het centrale deel, en hoge macro- en hyperbenthische biomassa's in het noordelijk deel).

Estuariene ecosystemen zoals de Oosterschelde kunnen veranderingen absorberen en zich eraan aanpassen, maar ze zijn ook heel kwetsbaar. In het Voordelta gebied werden veel hogere densiteiten genoteerd voor verschillende benthische organismen (vis, macro-invertebraten, macrobenthos en hyperbenthos) in de buitendelta van de Grevelingen in de periode 1988-'89 in vergelijking met de Oosterschelde buitendelta. Het toegenomen belang voor platvissen, vooral schar *Limanda limanda* en tong *Solea solea*, was waarschijnlijk in verband te brengen met de veranderde hydrodynamica sinds het afsluiten van het Grevelingen estuarium in 1971, waardoor de Grevelingen buitendelta als een 'val' fungeert en slib, detritus, eieren en larven vasthoudt. Nochtans kan de verhoogde kinderkamerfunctie van de buitendelta het verlies aan kinderkamer gebieden in het voormalige estuarium zelf niet goedmaken.

In de vorige hoofdstukken werden enkel de meest opvallende (en abundante) soorten macro-invertebraten besproken. In **Hoofdstuk 5** worden gedetailleerde patronen op korte en lange termijn voor verschillende soorten macro-invertebraten weergegeven, dit d.m.v. een vergelijking tussen de Westerschelde en de Oosterschelde estuaria, gebaseerd op kwartaalgegevens van de periodes 1988-'89 en 1999-2001. De hogere densiteiten in de laatste periode waren gecorreleerd met zachte winters, hogere densiteiten aan voedselbronnen, minder waterbouwkundige werken en grootte van het intertidaal habitat.

De diversiteitspatronen werden beïnvloed door saliniteit, sediment/habitat type, temperatuur en de introductie van vreemde soorten (vooral krabben). In de Oosterschelde werden 33 soorten macro-invertebraten genoteerd in de periode 1999-2001: 9 steurgarnalen, 9 krabben, 6 stekelhuidigen, 3 garnalen, 3 koppotigen, 2 heremietskreeften en 1 kreeft. De dominante soorten in de Oosterschelde waren slangsterren *Ophiura* species, grijze garnaal *Crangon crangon*, zeester *Asterias rubens*, strandkrab *Carcinus maenas* en heremietskreeft *Pagurus bernhardus*. De diversiteit in de Westerschelde was veel lager, met slechts 8 soorten: 4 krabben, 2 steurgarnalen, 1 garnaal en 1 heremietskreeft, met een overheersende aanwezigheid van *C. crangon*.

De seizoenale verspreidingspatronen in macro-invertebraten densiteiten in beide estuaria waren gerelateerd aan jaarlijkse veranderingen in temperatuur en concentratie opgeloste zuurstof. Een aantal soorten bleef slechts voor een korte periode (met hoogste densiteiten in de warmere seizoenen), terwijl anderen aanwezig waren in vrij hoge densiteiten doorheen het ganse jaar.

Verschillende ruimtelijke patronen in soortensamenstelling waren gerelateerd aan de gradiënten

in saliniteit-turbiditeit in de Westerschelde. Het (weder) voorkomen van de steurgarnaal *Palaemon longirostris* in de Westerschelde zou kunnen wijzen op een verbeterde waterkwaliteit.

In **Hoofdstuk 6** wordt geprobeerd om het voorkomen en de densiteit van 12 vis- en 3 macro-crustaceeën soorten in de Westerschelde te voorspellen aan de hand van een beperkt aantal omgevingsvariabelen (temperatuur, saliniteit, concentratie opgeloste zuurstof en turbiditeit, en/of de kwadratische effecten ervan). De meeste gegevens van de subtidale campagnes (1988-'91 en 1999-2001) werden hiervoor gebruikt. In een **addendum** worden deze modellen toegepast op gegevens van de Oosterschelde.

De maximum waarschijnlijkheid van voorkomen kon vrij goed worden voorspeld in beide estuaria d.m.v. soortgebonden (multipele) logistieke regressiemodellen. Sensitiviteit (% aanwezig voorspeld als aanwezig) en specificiteit (% afwezig voorspeld als afwezig) waren vergelijkbaar hoog in de meeste modellen, en validering toonde aan dat de modellen accuraat en robuust zijn. De gecombineerde interactie tussen de verschillende omgevingsvariabelen was krachtiger dan elke variabele afzonderlijk om het voorkomen van soorten te voorspellen, waarbij de seizoenale patronen overheersten op de ruimtelijke patronen. De voorspellingen werden niet verbeterd door toevoeging van andere variabelen (stroomsnelheid, prooidensiteiten van aasgarnalen, chlorofyl a of opgelost particulair materiaal).

De voorspellingen van de densiteiten van de afzonderlijke soorten d.m.v. multipele lineaire regressies aan de hand van dezelfde variabelen was slechts gedeeltelijk succesvol. Waarschijnlijk zijn andere variabelen nodig om betere voorspellingen te doen naar densiteiten en om de onderliggende causale verbanden weer te geven. De beste modellen werden geconstrueerd voor 7 soorten die gedurende langere tijd in het estuarium verbleven, maar met slechts één duidelijke densiteitspiek: schar *Limanda limanda*, brakwatergrondel *Pomatoschistus microps*, strandkrab *Carcinus maenas*, gewone zwemkrab *Liocarcinus holsatus*, bot *Platichthys flesus*, sprot *Sprattus sprattus* en dikkopje *Pomatoschistus minutus*. De densiteiten van deze soorten werden vooral gestructureerd door de omgevingsvariabelen. Deze "best-passende" modellen waren slechts beperkt toepasbaar op de Oosterschelde gegevens, doordat er geen ruimtelijke saliniteitsgradiënt meer bestaat in dit systeem, waardoor een aantal soorten een ander verspreidingspatroon vertoonde dan in de Westerschelde.

Voor acht soorten hadden de modellen maar een lage graad van voorspelbaarheid, namelijk voor deze die slechts een korte periode in het estuarium verbleven (steenbolk *Trisopterus luscus*, wijting *Merlangius merlangus* en kleine zeenaald *Syngnathus rostellatus*) of voor soorten met twee densiteitspieken (haring *Clupea harengus*, tong *Solea solea*, schol *Pleuronectes platessa*, grijze garnaal *Crangon crangon* en lozano's grondel *Pomatoschistus lozanoi*). Waarschijnlijk waren de densiteiten van deze soorten vooral gecorreleerd met de beschikbaarheid van voldoende prooien.

In **DEEL II** wordt een evaluatie gemaakt van het functioneren van de verschillende subhabitats in de Westerschelde als opgroeigebieden voor juveniele vis en macro-crustaceeën, en wordt de rol van hyperbenthische prooien – en van aasgarnalen in het bijzonder – voor de hogere trofische niveaus van het estuariene voedselweb onderzocht. Gegevens van verschillende sub- en intertidale boomkor campagnes werden gebruikt in Hoofdstukken 7 en 8 (aangevuld met 2 addenda).

In **Hoofdstuk 7** wordt d.m.v. ongeveer 1500 maaginhoud-analyses het dieet van 25 vissoorten in de Westerschelde onderzocht. Een artikel over de voedingsecologie van twee kabeljauwachtigen in de Voordelta wordt meegegeven als **addendum**.

Een aantal soorten, zoals dikkopje *Pomatoschistus minutus* en steenbolk *Trisopterus luscus* vertoonden een verandering in het dieet van roeipootkreeftjes (calanoide copepoden) naar aasgarnalen (mysids). Ook in de Voordelta veranderde het dieet van *T. luscus* en wijting *Merlangius merlangus* van roeipootkreeftjes over aasgarnalen naar garnalen en vissen met toenemende lengte van de vis. Zowel ontogenetische als seizoenale veranderingen in het dieet waren gekoppeld aan groei van de vissen en aan beschikbaarheid van de prooien. De totale jaarlijkse consumptie van beide kabeljauwachtigen tesamen in de Voordelta werd geschat op 0.47 - 0.57 g ADW m^{-2} jr^{-1}.

In de subtidale voedselwebben van de Westerschelde (zie Hoofdstuk 9), passeert de belangrijkste energiestroom tussen het tweede trofische niveau en de demersale vissen en macro-crustaceeën, vooral doorheen de 'pelagische' voedselketen. Kleine crustaceeën (roeipootkreeftjes, aasgarnalen, vlokreeftjes) vormden het belangrijkste onderdeel van het dieet, met een algemene dominantie van aasgarnalen. De meeste prooisoorten (inclusief soorten die normaal tot het endobenthos of the zoöplankon worden gerekend) waren ook algemene organismen in de hyperbenthische waterlaag. Verder vertoonden twee platvissen (schol *Pleuronectes platessa* en bot *Pleuronectes flesus*) een andere voedingsstrategie, door zich vooral te voeden in het intertidaal met vlokreeftjes (amphipoden), tweekleppigen (bivalven) en borstelwormen (polychaeten). Verschillende vissoorten en eveneens de grijze garnaal *Crangon crangon* (zie Hoofdstuk 8) gingen, naast een typisch subtidaal foerageergedrag, zich ook voeden met vlokreeften in het intertidaal.

Aasgarnalen werden in >50 % van de geanalyseerde magen van 19 van de 25 soorten terugge-

vonden. Aasgarnalen waren het belangrijkst in het dieet van *T. luscus*, *M. merlangius*, *P. minutus* en lozano's grondel *Pomatoschistus lozanoi*, en werden terugvonden in vrij hoge aantallen in het dieet van *P. flesus*, rode poon *Trigla lucerna*, haring *Clupea harengus* en *P. platessa*. Deze soorten voedden zich vooral met de brakwateraasgarnaal *Neomysis integer*, terwijl *Mesopodopsis slabberi* (aanwezig in 35 % van de grondelmagen) en *Gastrosaccus spinifer* (aanwezig in 25 % van de magen van kabeljauwachtigen) waren van ondergeschikt belang. Er werd geschat dat slechts 1 % van de aanwezige aasgarnalen populaties werd weggenomen per dag door de locale demersale visgemeenschap.

In **Hoofdstuk 8** worden de diurnale, seizoenale en ruimtelijke patronen in het dieet van de grijze garnaal *Crangon crangon* in de Westerschelde voorgesteld, gebaseerd op twee 24-uurs campagnes in September 1991 in het brakke subtidaal, seizoenale bemonsteringen in het mariene en brakwaterdeel van het subtidaal in de periode 1999-2000, en maandelijkse staalnames in 1992. Een artikel dat handelt over voedselwebben in de Westerschelde werd eveneens opgenomen in een **addendum**.

Van alle maaganalyses waren er 36 % leeg, 33 % hadden weinig (sterk verteerde) prooiresten (vooral afkomstig van crustaceeën) in de maag en 31 % bevattte veel (halfverteerde) prooi-items. De minimum en maximum dagelijkse consumptie bedroeg 1-5 % lichaamsgewicht per dag in het subtidaal en 4-14 % lichaamsgewicht per dag in het intertidaal. De jaarlijkse consumptie was 1-8 g ADW m^{-2} jr^{-1} zowel sub- als intertidaal.

Op een dagelijkse schaal vertoonden densiteit, voedingsintensiteit en prooidiversiteit gemengde tidale-diurnale patronen, waarbij het effect van de getijwerking (tidaal) overheerste over het diurnale effect. Bij opkomend tij werd meer gegeten en was de trofische diversiteit hoger. Aasgarnalen (vooral *Neomysis integer* en *Mesopodopsis slabberi*) waren de belangrijkste prooi-items, zowel 's nachts als overdag. Er wordt verondersteld dat *C. crangon* voornamelijk 's nachts foerageert in de hyperbenthische waterlaag en zijn dieet aanvult met enige prooien vanuit de epibenthische laag gedurende de dag.

Op een seizoenale schaal waren densiteit en prooidiversiteit het hoogst tijdens de zomer, zowel sub- als intertidaal. De invloed van het getij maskeerde voor een stuk de seizoenale variatie in maagvulling. Alhoewel we weten dat er verschillende voedselwebben bestaan in het mariene en brakwaterdeel van de Westerschelde, wordt dit niet echt weerspiegeld in de hogere trofische niveaus. Aasgarnalen waren belangrijke prooien in de lente en de zomer in het subtidaal doorheen het estuarium. Enkel de soorten veranderden: vooral *Gastrosaccus spinifer* in het mariene deel en *N. integer* en *M. slabberi* in het brakwaterdeel. In deze brakwaterzone werden aasgarnalen vervangen door vlokreeftjes (*Corophium* en *Bathyporeia* soorten) in de herfst en de winter, wat overeenkwam met de seizoenale patronen in densiteiten en beschikbaarheid van de prooien.

Op een ruimtelijke schaal was in het brakwaterdeel de prooidiversiteit hoger in het intertidaal dan in het subtidaal. Aasgarnalen werden slechts af en toe gepredeerd in het intertidaal, waar roeipootkreeftjes gradueel vervangen werden door vlokreeftjes (*Corophium*) in het dieet, met toenemende grootte van *C. crangon*.

De predatie-impact door garnalen op de populaties aan aasgarnalen is veel hoger dan deze door de visgemeenschap: gemiddeld werd 10 tot 35 % van de aanwezige aasgarnalen geconsumeerd per dag door *C. crangon*.

Uiteindelijk wordt in **Hoofdstuk 9** een overzicht gegeven van de kinderkamerfunctie van de Westerschelde en de Oosterschelde voor demersale vissen en macro-invertebraten, gebaseerd op alle gegevens die in dit proefschrift worden voorgesteld, inclusief een verband tussen het voorkomen van (post)larvale en juveniele levensstadia in het subtidaal van beide estuaria, en in verschillende subhabitats in het Westerschelde estuarium.

De larven en vroeg-postlarvale levensstadia van 17 vissen en 11 macro-crustaceeën werden genoteerd in de Westerschelde en/of de Oosterschelde, vooral in de lente en in de intertidale brakke schorkreken. Er werd een duidelijke seizoenale opeenvolging vastgesteld van verschillende levensstadia (postlarve – juveniel – onrijp – adult) van verschillende soorten vissen en macro-crustaceeën in diverse subhabitats (intertidale schorkreken – intertidale banken – subtidaal).

De biodiversiteit is gekoppeld aan het gebruik en de beschikbaarheid van habitats. In totaal werden 96 vissoorten genoteerd gedurende de laatste twee decennia in de verschillende habitats, 75 soorten in de Oosterschelde en 74 soorten in het Schelde estuarium (inclusief de tidale zone stroomopwaarts van de Westerschelde).

Het voorgestelde proefschrift kan gezien worden als een basisstudie over de vis- en macro-invertebraten gemeenschappen in de Westerschelde en de Oosterschelde. De thesis suggereert dat beide estuaria een significante rol hebben als kinderkamergebieden voor verschillende soorten vissen en macro-invertebraten. De analyse van de structuur en het functioneren van de demersale vis- en macro-invertebraten gemeenschappen in de Westerschelde en Oosterschelde estuaria op verschillende ruimtelijke en temporele schalen, leverde 10 belangrijke conclusies op die doorheen de verschillende hoofdstukken van dit proefschrift worden weergegeven. Tenslotte worden een aantal aanmerkingen op het proefschrift en een aantal aanbevelingen voor toekomstig onderzoek gegeven.

CHAPTER 1 INTRODUCTION, OBJECTIVES AND OUTLINE OF THE THESIS

K. Hostens

Abstract. *The thesis focuses on the nursery function of the Westerschelde and Oosterschelde estuaries for demersal fish and macro-invertebrate species. The main aim of the thesis is to provide a baseline about the higher trophic levels for future process studies in the Delta area. More specifically, both structural and functional patterns in several population parameters (density, biomass, growth, biodiversity, food and feeding behaviour) are investigated at community and species levels, and at different temporal (short-, mid- and long-term) and spatial (between and within estuaries) scales. This introductory chapter gives a general description of the epibenthic assemblages and a short overview of the factors on which the nursery function of a system depends. The study area is described and the major engineering works in the Delta area are summarized. An overview of the different sampling methodologies and of the available and used datasets is given. This chapter finishes with the main objectives and an outline of the thesis.*

1.1 Introduction

Shallow coastal areas, and especially estuaries, are widely recognized as important nurseries for juvenile fish and macro-crustaceans, feeding areas for adults and migration routes for diadromous species (McHugh 1967, de Sylva 1975, Pihl & Rosenberg 1982, Haedrich 1983, Elliott *et al.* 1990, and Chapter 2-Add.2). Recently, the status of European estuaries and brackish habitats in relation to fish and macro-crustaceans has been thoroughly reviewed in a collaborative work from 18 laboratories across 11 countries, based on data from 26 estuarine systems (Elliott & Hemingway 2002). The contributions concerning the Westerschelde and Oosterschelde estuaries to this review, resulting from a FAIR concerted action (CT96-1634, *Commercial Fish in Estuaries – Priorities for Management and Research*), were partly based on data presented in this thesis.

Estuaries are characterized by a low diversity and dominance of only a few macro-invertebrate and juvenile fish species (McLusky 1989, Wootton 1992). The most abundant fish and macro-invertebrate species in estuaries are eurytopic, euryhaline, and present at high numbers during their early life history for different periods of the year. To assess the nursery function of the Westerschelde and Oosterschelde estuaries, both structural and functional patterns have to be investigated, taking into account density dependent (*e.g.* competition, predation) and independent (environmental) factors (Blaber & Blaber 1980, Elliott & Taylor 1989, Marchand 1993, Gibson 1994). Therefore, information is needed on several biotic and abiotic compartments. The main forcing variables structuring the fish communities are given in Fig. 1.1. The present study is largely rooted in the multidisciplinary research on the Westerschelde and Oosterschelde. Both estuaries, but mainly the Westerschelde, are among the best-studied systems in Europe (and probably in the

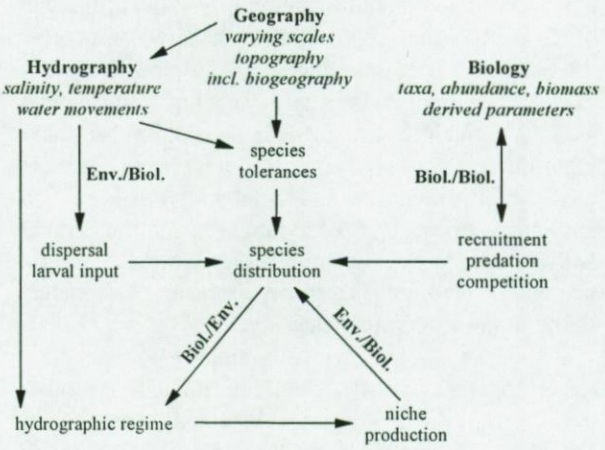

Fig. 1.1 Main forcing variables on structuring fish communities (from Elliott & Hemingway 2002)

world). One of the main reasons is the large anthropogenic pressure on both systems. The Westerschelde and Oosterschelde estuaries are part of the Delta area in the southwest part of the Netherlands. The human impact on this area is quite high: poldering for agriculture and industry, dykes and dams for safety and freshwater hold, dredging for the ever-growing shipping industry, commercial fisheries on demersal fish and shrimps in the Westerschelde and mussels and oysters in the Oosterschelde. All these activities lead to a quantitative loss of habitats for growing juvenile fish and macro-invertebrates. The direct consequences of the human impact, such as untreated organic waste loads, industrial pollution and fresh water and tidal reduction, contribute to the diminishing quality of the Delta area. This introductory chapter gives an overview of the study area and the major engineering works in the Delta area.

In their report on habitat structures and communities, Van Damme *et al.* (1999) described the research effort on fish in the Schelde estuary as fragmented, sampled by means of different methodologies, at different places and times, or only partly reported. Of course, to study the different aspects of a nursery, different sampling periods and methodologies are required. Moreover, long-term records of biological data are necessary to differentiate between natural changes in the ecosystem and those caused by humans (Wolfe *et al.* 1987). An overview is given on the available and (partly) used data, and on the different methodologies to sample different life stages of demersal fish and macro-invertebrates in the different subhabitats of the Westerschelde and Oosterschelde estuaries. Finally, the main objectives and the rationale of the thesis are given.

1.2 Description of the demersal fish and macro-invertebrate assemblages

In earlier studies the demersal fish and macro-invertebrate assemblages have been termed the epibenthos or epibenthic community. This group can be defined as the larger animals that live on or near the bottom to rest, hide, feed or reproduce. Pragmatically, all animals caught with a beam trawl, which are less efficiently caught near the bottom with any other device, are considered to belong to the epibenthos. Mainly juveniles and older individuals of fish and macro-invertebrates are caught in shallow coastal and estuarine areas. Today, we prefer to use the term demersal fish and macro-invertebrate assemblage, living in the epibenthic waterlayer.

Fish species typically belong to the Pleuronectiformes (flatfish), Gobiidae (gobies) and other Perciformes, Clupeiformes (clupeoids), Gadiformes (gadoids), Syngnathiformes (pipefish), Scorpaeniformes, and a number of other taxonomic groups.

Macro-invertebrates are much more abundant than the fish fauna in estuarine and shallow coastal areas (*e.g.* Pihl 1985, Bamber & Henderson 1994, Beyst *et al.* 2002). However, till the 1980s the macro-invertebrates were rarely integrated into fish studies (Chapter 2-Add.2). In earlier studies discussed in this thesis, only the four most conspicuous epibenthic invertebrates were taken into account (i.e. brown shrimp *Crangon crangon*, starfish *Asterias rubens* (only in the Oosterschelde), shore crab *Carcinus maenas*, and swimming or flying crab *Liocarcinus holsatus*). During later surveys, all macro-invertebrates were quantified, comprising different species from the echinoderms, caridean shrimps and prawns, brachyuran and anomuran crabs, and cephalopods.

Other invertebrate species are quite common in the beam trawl samples from the Oosterschelde, but these were not considered as part of the 'epibenthic assemblage', as they are either sessile or planktonic organisms. The following groups were not quantified: tunicates (a.o. *Styela clava, Ciona intestinalis* and *Ascidiella aspersa*), cnidarians (also in the Westerschelde, a.o. *Aurelia aurita*, *Chrysaora hysoscella* and *Cyanea lamarckii*), sea anemones (a.o. *Actinia equinea*), bivalves (*Mytilus edulis*, *Ostrea edulis* and *Crassostrea gigas*), gastropods (a.o. *Littorina littorea*, *Crepidula fornicata* and *Nucella lapillus*), polychaetes (a.o. *Aphroditae* and *Harmothoe* species), and nudibranchs (a.o. *Aeolidia papillosa* and *Elysia viridis*).

Older and/or mature fish only sporadically enter shallow coastal and estuarine areas. The thesis mainly focuses on juvenile fish, i.e. the O- and I-group, and the juvenile and adult stages of the macro-invertebrates. In the final synthesis, the (post)larval stages of the most abundant fish and macro-invertebrate species are taken into account as well, to give a complete overview of the seasonal and spatial distribution of the demersal fish and macro-invertebrate assemblage. Larvae and postlarvae of fish and invertebrates are more effectively caught with a hyperbenthic sledge, and are part of the merohyperbenthos. Together with the permanent hyperbenthos (mainly mysids and amphipods), they constitute the hyperbenthos. These small organisms usually live close to the bottom in the hyperbenthic waterlayer, at least during part of the day. See Mees & Jones (1997) for a review, and Beyst *et al.* (1999) for data on post-larval fish in the Dutch Delta.

1.3 The nursery function

Nurseries are defined as areas where juveniles aggregate, are spatially or temporally separated from the adults, and where their survival is enhanced through better feeding conditions, optimal growth and/or ref-

uge opportunities. Recruitment to the adult or subadult populations follows the emigration from these nurseries after attaining a well-defined length class (Pihl *et al.* 2002).

The nursery function of a system for juvenile fishes and macro-invertebrates is dependent on several factors. Firstly, the nursery function depends on the transport and retention efficiency of (post)larvae and juveniles towards and within the estuary. Larvae and/or postlarvae are attracted to the estuarine system, and either actively or passively find suitable habitats and protection from predators (*e.g.* van der Veer & Bergman 1986, Drake & Arias 1991, Jager 1999). For example, brown shrimp *Crangon crangon* are transported to the Westerschelde as zoea larvae, migrate into the brackish intertidal saltmarsh creeks shortly after metamorphosis to the postlarval stage, and recruit after a few weeks to the deeper regions of the estuary proper as juveniles (Cattrijsse *et al.* 1997).

Secondly, the nursery function is dependent on habitat availability, in relation to diversity, growth and survival of the juveniles. In trying to simplify our understanding of a nursery, the functional guild concept was developed (*e.g.*McHugh 1967, Elliott & Taylor 1989, Whitfield 1999). Fish can be grouped into bottom-dependence and substratum preference guilds, or into reproductive, feeding and ecological guilds, indicating the usage of the estuarine habitats by the fish and the importance of an estuary for fish (Elliott & Dewailly 1995). The different habitats of an estuary (*e.g.* subtidal - intertidal, soft – hard substrate, saltmarsh – seagrass – reed beds, tidal freshwater) are inhabited during different periods by different species and several life stages of fish and macro-invertebrates. Multivariate statistical techniques are widely used to unravel the spatial and temporal patterns in fish and macro-invertebrate assemblages in relation to the environment (*e.g.* Pihl 1986, Marshall & Elliott 1998, and Chapter 2-Add.2). Most studies showed that salinity and substratum/exposure were among the most important variables in structuring the epibenthic assemblages (*e.g.* Henderson 1989). Recently, a number of studies tried to relate single species presence and abundance to changes in environmental parameters (*e.g.* Attrill *et al.* 1999).

Thirdly, the nursery function is largely dependent on food availability. Estuaries are highly productive systems, so juvenile (and adult) fish and macro-invertebrates can find plenty of suitable prey organisms (*e.g.* Henderson *et al.* 1992, Moreira *et al.* 1992, Marshall 1995). In the Westerschelde estuary, two food chains have been demonstrated, a phytoplankton driven food chain in the mouth or marine part and a much more important detritus (and bacterial) based food chain in the brackish part (Hummel *et al.* 1988b, Soetaert & Herman 1995a, also Chapter 8-Add. and Chapter 9). The link between primary producers and fishes and macro-crustaceans, is composed of the secondary trophic levels. These consist mainly of benthic (in- and epifaunal) and zooplanktonic/hyperbenthic organisms (*e.g.* de Sylva 1975, Hemingway & Elliott 2002).

1.4 Study area

1.4.1 The Dutch Delta

The thesis is mainly based on data from the Westerschelde and the Oosterschelde. Both estuaries are located in the southwest of the Netherlands (51°20'-51°41'N, 3°34' - 4°14'E), and are part of the so-called Dutch Delta area (Fig. 1.2). In this area, three major European rivers, the Rhine, Meuse and Schelde, enter the North Sea. Every chapter includes a short description of the study area, as they will be or have been submitted as such for publication in the international literature. In this introductory chapter, a short overview is given of the major engineering works and the geomorphology (including the more recent evolution) in the Southern Dutch Delta area, with a basic characterisation of the Westerschelde and Oosterschelde estuaries.

A definition of an estuary is given by Day *et al.* (1989): "an estuarine system exists of a coastal embayment, with a narrow connection to the ocean, and at least a temporal free connection with the terrestrial system." They distinguished 3 regions: (1) a turbid coastal area in the mouth of the estuary; (2) a mixed zone (the estuarine proper), characterized by a strong mixing of the water masses and strong gradients in physical, chemical and biotic components; (3) a fluvial zone (freshwater tidal), characterized by the absence of saltwater, but subject to the tides.

According to this definition, the Westerschelde, Oosterschelde and Voordelta area can be seen as estuaries *sensu latu*. However, a distinction between 5 types of 'estuaries' was made, ranging from real and estuarine deltas, over real estuaries, to estuarine and marine lagoons. A definition of an estuary *sensu strictu* was given by Pritchard (1967): "an estuary is a semi-enclosed coastal water body, which has a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage".

The Schelde valley was already colonized around 6000 B.C., but the formation of the Westerschelde only started between 800 and 1000 A.D. (de Mulder & van Strydonck 2000). Landclaim for agricultural reasons started around 1100 A.D. in the Dutch Delta, with a peak of poldering between 1500 and 1600 (Mol 1995). Only since 1870 the Westerschelde and Oosterschelde estuaries got completely separated (Antrop & van der Reest 2001). During the 20th century harbour construction, dyke re-

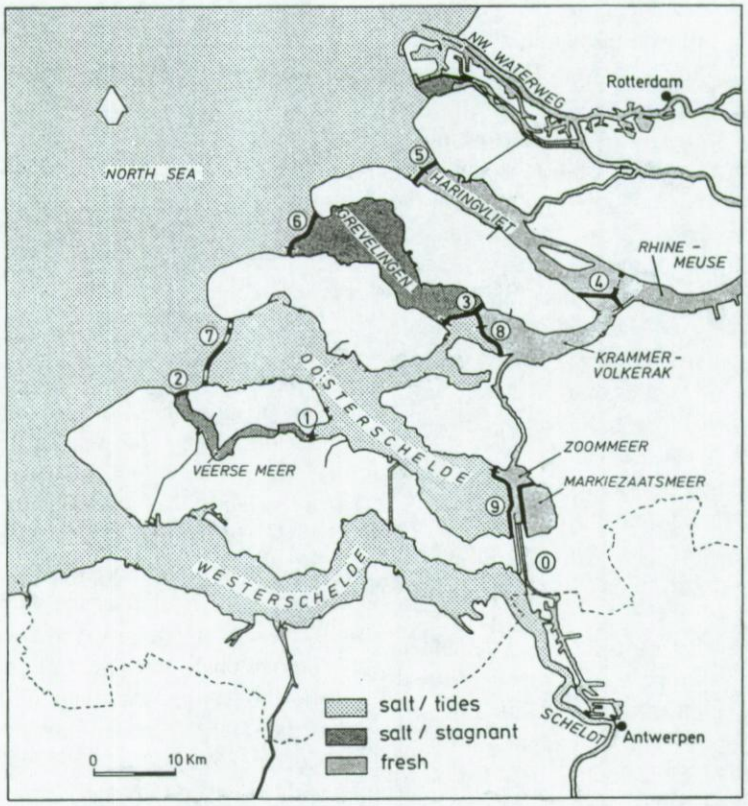

Fig. 1.2 The Dutch Delta area (SW Netherlands), with an indication of the major engineering works. 0 = Kreekrakdam (1867); 1 = Zandkreekdam (1960); 2 = Veersegatdam (1961); 3 = Grevelingendam (1964); 4 = Volkerakdam (1969); 5 = Haringvlietdam (1970); 6 = Brouwersdam (1971); 7 = Oosterschelde storm-surge barrier (1986); 8 = Philipsdam (1987); 9 = Oesterdam (1986). Zoommeer and markiezaatsmeer were separated in 1983 (taken from Nienhuis & Smaal 1994b)

enforcement and poldering were the main causes for landclaim. During the past two centuries 150 km² of marshes and mudflats around the Schelde disappeared (Mol 1995). After the catastrophic storm floods of 1953, the Dutch Delta area in the southwest Netherlands underwent dramatic changes as different sea arms were closed off. This resulted in the creation of freshwater, brackish and salt lakes, marine embayments and tidal deltas.

The engineering works in the Delta area started with the construction of compartmentalisation dams to reduce the tidal influence in the region. In 1960-61, the former estuary 'Veerse Gat' was closed (zandkreekdam and Veerse dam) and transformed into a stagnant brackish lake 'Veerse Meer', with a loss of 42 km² of estuarine habitat. The next compartmentalisation dams cut off the riverine influence of the Rhine and Meuse in the former 'Grevelingen' (1964, Grevelingendam) and 'Oosterschelde' (1969, Volkerakdam) estuaries, turning both systems into marine bays. Next, the former estuaries 'Haringvliet' (1970, Haringvlietdam) and 'Grevelingen' (1971, Brouwersdam) were closed off from the sea and transformed into a non-tidal freshwater system and the stagnant salt lake 'Grevelingenmeer' (with an artificial flow regime through sluices), respectively. This resulted in a total loss of 65 and 140 km² estuarine habitat (Visser 1995). In 1986, the storm-surge barrier in the mouth of the Oosterschelde reduced the tidal range and tidal volume, with a loss of 75 km² of intertidal habitat (Nienhuis & Smaal 1994b). The last Delta works included the construction of two dams (1986, Philipsdam; 1987, Oesterdam), and the creation of two freshwater lakes ('Volkerak/Zoommeer' and 'Markiezaatsmeer'), with a loss of 83 and 21 km² estuarine habitat, respectively (Wanningen & Boute 1997, Haas 1998). With the reduction of the freshwater input to a minimum, the former Oosterschelde estuary was transformed into a marine bay.

As a result of the Delta works, the tidal currents at the seaward side of the dams were largely reduced. The tidal gullies in front of the former estuaries were filled and new sandbanks were formed, leading to the creation of marine tidal deltas. The formation of the deltas is mainly induced by ebb-tidal currents (Louters *et al.* 1991). This dynamic area is called the 'Voordelta', and stretches from the 'Nieuwe Waterweg' in the north to the mouth of the Westerschelde in the south, with a marine boundary 10 to 15 km seaward from the coastline, arbitrarily defined by the depth contour of 10 m below mean tidal level (MTL, as defined for Amsterdam). As such, the Voordelta is composed of the ebb-tidal deltas of the former Oosterschelde, Grevelingen and

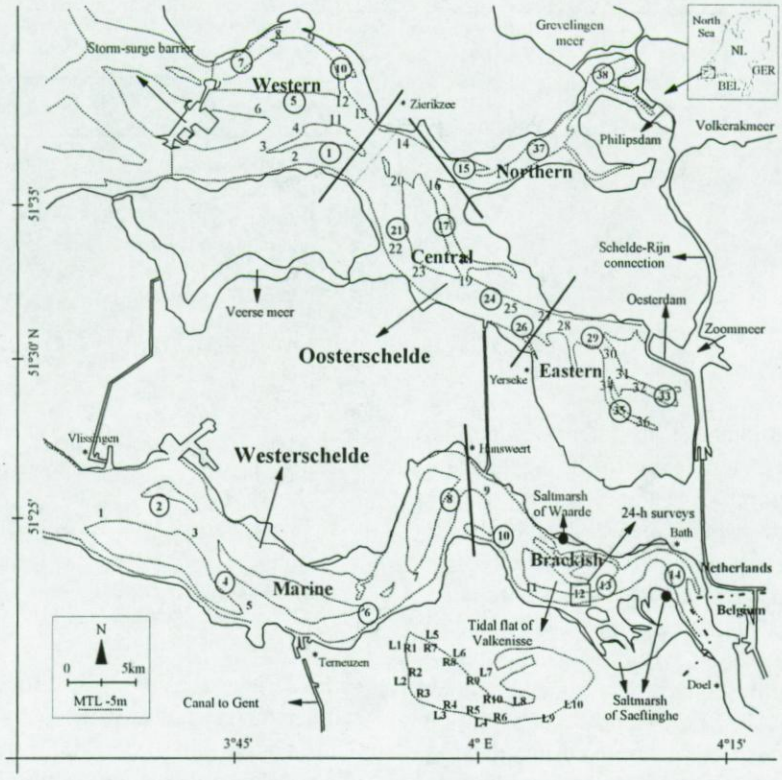

Fig. 1.3 The Westerschelde and Oosterschelde estuaries, with an indication of the sampling locations during the different surveys. See text and Table 1.2 for an explanation

Haringvliet estuaries, which have lost their estuarine 'mouth' character.

The Westerschelde remained open at both the river and sea side, for international shipping purposes (Nienhuis & Smaal 1994a). The complementary Sigma works (started in 1977) in the Schelde estuary, mainly consisted of dyke elevation and reenforcement, and the creation of 13 controlled inundation areas in the upper part of the estuary (the Zeeschelde) and its major tributaries (Rupel, Durme and Dender) (Van Damme & Meire 2001). In 1994, 75 % of the dyke works were completed and most inundation areas were constructed. The consolidation of almost all borders by concrete dykes inhibits the natural processes of erosion and sedimentation, and leads to fixation of the main subtidal channel (Mol 1995). According to both definitions of an estuary, only the Westerschelde can be regarded a true estuary.

1.4.2 The Westerschelde estuary

The Westerschelde consists of the lower and middle parts of the Schelde estuary and covers 310 km² (Fig. 1.3). The Westerschelde stretches along 55 km from the mouth (arbitrarily situated near Vlissingen, 5000 m width) to the Dutch-Belgian border (near Bath, 350 m width), and can be divided into two subareas near Hansweert: the western (marine) and eastern (brackish) part. The tidal zone upstream the border is called the Zeeschelde (105 km long till Gent and a surface of 44 km²), which can be divided near Antwerp into the 'lower' and 'upper' Zeeschelde.

The Westerschelde is characterized by a marked salinity gradient (range 4-32 psu during the studied period). It is a well-mixed water body, and the residence time of the water is about 120 tidal cycles in the brackish zone and 10 to 15 days in the most seaward region (Soetaert & Herman 1995b). Salinity zones in the estuary remain relatively stable and are maintained in more or less the same position throughout a tidal cycle, but can shift over a few km between seasons (Heip 1989a). River discharge is largely dependent on rainfall, and highest during winter (on average 180 $m^3 s^{-1}$) and lowest in summer (60 $m^3 s^{-1}$) (Baeyens *et al.* 1998). The Westerschelde is a macrotidal estuary, with an average tidal amplitude of 3.8 m near Vlissingen and 4.9 m near Bath (Claessens 1988). Maximum ebb and flood current velocities vary between 1 and 1.5 m s^{-1} at average neap and spring tides, respectively (recalculated from Anonymous 1992).

Turbidity is high, with 7.5 10^5 tonnes yr^{-1} of fluvial fine sediments and 9 10^4 tonnes of marine suspended matter entering the system, which accumulate in the maximum turbidity zone in the Lower Zeeschelde (Anonymous 1998, Baeyens *et al.* 1998). The Westerschelde is a nutrient-rich system. The ongoing discharge of untreated wastewater through the Rupel and the Zenne, is the main source of high organic loads in the Schelde estuary. This leads to

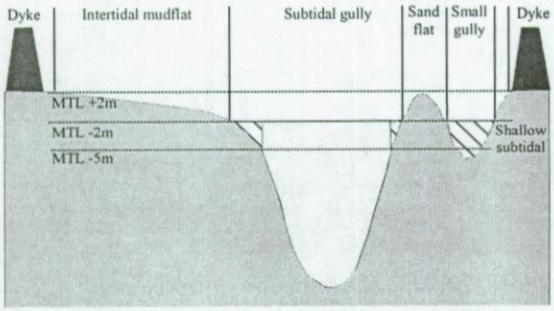

Fig. 1.4 Schematic drawing of the different habitats in an estuary

heterotrophic respiration due to intense microbial activities, and oxygen deficiency in the upper estuary, mainly during summer (Heip *et al.* 1995, Van Eck *et al.* 1998). However, in the Westerschelde the water column is relatively well oxygenated, with concentrations of dissolved oxygen seasonally changing between 6 and 10 mg.l^{-1} (Chapter 5). Industrial pollution is still very high in the Schelde estuary. Micropollutants (mainly bound to suspended solids), like heavy metals, PAHs, PCBs and organochlorine pesticides, show a decreasing trend during the last decade, but concentrations are still elevated, both in the water column and in the sediments throughout the estuary (Van Zoest & Van Eck 1990, Anonymous 1998).

The Westerschelde is characterized by multiple channels (average depth 15-20 m below MTL) surrounding large intertidal flats, bordered by mudflats and saltmarshes (Van Maldegem *et al.* 1993). A schematic drawing of the different habitats in an estuary is given in Fig. 1.4. The division between the subtidal gullies and intertidal flats and marshes lies around mean low water (MLW or MTL –2 m). The transition zone from subtidal to intertidal can further be divided into 'shallow' (MTL –5 m to –2 m) and 'intertidal' (MTL –2 m to +2 m) water masses (Mol *et al.* 1997). The saltmarshes are intersected by several intertidal creeks of different sizes. The main shipping channel actually exists of successive ebb-dominated gullies, while the smaller side channels are flood-dominated.

The Westerschelde forms an important connection between the North Sea and 4 major harbours: Vlissingen, Terneuzen, Antwerpen en Gent (5-8 10^4 ship movements per year). To maintain (and deepen) the main channel, the dredging intensity is very high, up to 8 10^6 m^3 per year (Vroon *et al.* 1997). Due to this continuous dredging, shallow subtidal areas and intertidal mudflats (mainly in the brackish part) disappear, while the extent of deep subtidal areas and high sandflats increases (Mol 1995). Moreover, about 100 10^6 m^3 of sand has been extracted from the Westerschelde since 1950, which may play a determining role in the morphological development of the estuary on a long time scale (100 years) (Vroon *et al.* 1997). Disposal of the dredged material leads to a gradual increase in tidal elevation of flats and saltmarsh creeks, also with a subsequent loss of intertidal habitat. Pihl *et al.* (2002) defined 9 subhabitats of importance for estuarine fish. The areal extent of the different habitats in the Westerschelde is given in Table 1.1. The subtidal surface area amounts to 130 km² in the marine part and 40 km² in the brackish part. The subtidal is characterized by sandy sediments: median grain size 330 ± 97 µm in the marine part and 240 ± 55 µm in the brackish part (Chapter 5). The intertidal covers 35% of the total surface area, with 49 km² sandflats and 33 km² mudflats (Anonymous 1998). Another 32 km² is allocated to shallow subtidal water. Several smaller sandflats got aggregated to larger entities, and have steeper borders than during the 1960s (Mol *et al.* 1997). The lower parts of the intertidal are mostly poor in silt concentration, while the upper parts are characterized by high silt concentrations. The high intertidal part of the brackish sandflat of Valkenisse had a mixed sand-silt sediment, with a median grain size 168 ± 40 µm and an average concentration of 10 % silt (Chapter 8). Most of the saltmarsh surface area is part of one of the largest European saltmarshes 'Verdronken Land van Saeftinghe' (25 km²).

Table 1.1 Areal extent of the different subhabitats in the Westerschelde and Oosterschelde (km²)

Subhabitat	Westerschelde[a]	Oosterschelde
Tidal freshwater	(30)	
Reed beds	(5)	
Saltmarsh	25	6
Intertidal soft substratum	83	68
Intertidal hard substratum		11
Subtidal soft substratum	170 +32[b]	223
Subtidal hard substratum		1
Subtidal seagrass beds		1
Biogenic reefs		41
Total surface	**310 (+35)**	**351**

[a] values between brackets are part of the Schelde estuary but not of the Westerschelde
[b] + shallow subtidal area

Primary production is partly derived from phytoplankton (*e.g.* diatoms, dinoflagellates) and microphytobenthos (mainly intertidal benthic diatoms), although annual gross bacterial production exceeds the net primary production, even in the marine part (Goosen *et al.* 1997). Zooplankton (mainly copepods) and hyperbenthic organisms (mainly mysids and amphipods) are present in high numbers in the subtidal (*e.g.* Mees *et al.* 1993b, Soetaert & Van Rijswijk 1993). Meiobenthic (nematodes) and macrobenthic organisms (mainly bivalves, polychaetes and amphipods) are abundant in the intertidal (*e.g.* Ysebaert *et al.* 1993, Steyaert *et al.* 2001). The

whole estuary is of international importance for several life stages of different bird species (*e.g.* Ysebaert 2000). Recently, the number of sea mammals (mainly seals) increased again to some 20 individuals (Witte *et al.* 1998). At several places in the Westerschelde commercial fisheries exist, mainly on sole and plaice in the delta (Vlakte van de Raan), on shrimp in the subtidal and on cockles on the intertidal flats throughout the Westerschelde. Also, a small-scale fishery on eel and sprat exists in the Zeeschelde. Recreational shipping and fishing are of minor importance, and mainly take place in the mouth near Vlissingen (Anonymous 1998).

More details on the morphological, physical, chemical and ecological properties of the Westerschelde estuary are given in Hummel *et al.* (1988a), Meire & Vincx (1993), Heip & Herman (1995), Anonymous (1998), and Van Damme *et al.* (1999).

1.4.3 The Oosterschelde estuary

The Oosterschelde is a marine bay with a total surface area of 350 km² (Fig. 1.3). The Oosterschelde is directly connected with the Westerschelde through a channel between Hansweert and Yerseke, and indirectly through sluices in the Zoommeer. The distance form the storm-surge barrier in the mouth to the Oesterdam in the east and to the Philipsdam in the north equals 40 km. The Oosterschelde can be divided into four subareas: the western part in the mouth, downstream from the Zeeland Bridge, the central and eastern (or basin) parts divided near Yerseke, and the northern part covering the Keeten-Mastgat area (or Noordelijke Tak).

After the engineering works, typical estuarine gradients have disappeared. The mean freshwater load dropped from 70 to <20 $m^3 s^{-1}$, leading to a high and stable salinity of 30-34 psu (Haas 1998). The mean tidal volume decreased with 30% to 900 10^6 m^3, the tidal amplitude near Yerseke is 3.3 m, and the maximum current velocity is 1 m s^{-1} (Oosterlaan & Zagers 1996). The residence time of the water is 10-100 days, leading to high sedimentation of organic matter and high water transparency (Nienhuis & Smaal 1994b). The Oosterschelde is a nutrient-poor (oligotrophic) system. Concentrations of micropollutants in the water column are generally low, and polluted sediments of the harbours have largely been treated (van Berchum & Wattel 1997). Dissolved oxygen concentrations range between 7 mg l^{-1} in summer and 10 mg l^{-1} in winter-spring (Chapter 5).

The Oosterschelde is characterized by multiple tidal channels, mudflats and large intertidal sandy shoals. Due to a reduced tidal volume, the Oosterschelde changed from a sand-exporting to a fine sediment-importing system (ten Brinke *et al.* 1994). No dredging is necessary, although there is a high commercial shipping activity (5 10^4 ship movements per year) mainly on the north-south connection through the Oosterschelde. The subtidal channel has a so-called 'sediment hunger', i.e. the need of 500 10^6 m^3 of sand to adjust the channel surface to the reduced current velocities. Erosion of the intertidal area has been predicted to be an ongoing process with a reduction of 1.5 % per 5 years (van Berchum & Wattel 1997). The subtidal surface area amounts to 223 km² of soft sediments and only 1 km² of subtidal seagrass beds and hard substratum each (Pihl *et al.* 2002, Table 1.1). The subtidal sediment mainly consists of sand with a median grain size of 187 ± 37 µm (and on average 12 ± 9 % silt), except in the northern part where the sediment is much finer (median 45 ± 14 µm and silt concentration 57 ± 7 %) (Chapter 5). The intertidal area covers 118 km² with 58 % soft sediments, 33 % biogenic reefs and 9 % hard substratum. The latter is mainly covered by brittlestars, ascidians and sponges (Leewis *et al.* 1994). Saltmarshes suffered most from the engineering works, with the total surface area being reduced from 17 to 6 km² (Nienhuis & Smaal 1994b).

Primary production in the Oosterschelde is primarily derived from phytoplankton (including *Phaeocystis* blooms) subtidally and microphytobenthos intertidally (Wetsteyn & Kromkamp 1994, de Jong *et al.* 1994b). Meiobenthic nematodes are mainly present intertidally, meiobenthic and zooplanktonic copepods subtidally (Smol *et al.* 1994, Bakker & van Rijswijk 1994). Hyperbenthic organisms (mainly ctenophores and crab larvae) are abundant in the subtidal (Chavatte 2001). Macrobenthic densities (mainly gastropods, oligochaetes and polychaetes) are highest intertidally, macrobenthic biomasses (mainly oysters and mussels) are highest in the shallow subtidal (Stikvoort 1997). Macrophytes (mainly green macro-algae) are found both intertidally and subtidally (van Berchum & Wattel 1997). The Oosterschelde is one of the most important bird sites within the Delta area (Meininger *et al.* 1997). A small number of seals (20 individuals) is found mainly on the intertidal flats in the western part (van Berchum & Wattel 1997). The extensive flats and the surrounding shallow subtidal areas in the Oosterschelde are especially used for shellfish farming. The intertidal areas are important for the exploitation of cockles, while after the engineering works the shallow subtidal areas became important for the farming of oysters and mussels. The high densities of these macrobenthic suspension feeders and their feeding activity, result in a dominant and potentially controlling role in the main nutrient fluxes in the Oosterschelde (*e.g.* Herman & Scholten 1990). Recreational shipping and scuba-diving are largely extended. The commercial (fish) fishery is limited, and recreational fishing seems to decrease (van Berchum & Wattel 1997).

More details on the morphological, physical, chemical and ecological properties of the Ooster-

schelde estuary are given in Nienhuis & Smaal (1994a) and van Berchum & Wattel (1997).

1.5 sampling methodology

The sampling strategy depends on the survey objectives, the logistics and restrictions, substratum and habitat type, the hydrodynamic regime, the spatial and temporal coverage, and the life stage and distribution in the water column of the biota, all interrelated with net efficiency (Hemingway & Elliott 2002). Several authors have summarized the methods required for sampling fish assemblages or the associated factors required to interpret fish data. A complete overview of 'all' sampling techniques for different life stages and different estuarine habitats, is given in Hemingway & Elliott (2002).

Most of the thesis is based on data gathered in the subtidal with a 3-m beam trawl, equipped with a fine-meshed net (5x5 mm). Again, as most chapters will be published in international journals, a 'material and method' chapter is included in every chapter, although the information on sampling is mostly limited. Moreover, in the last chapter some extra material has been used from other studies (*e.g.* research on hyperbenthos and saltmarshes). Therefore, a complete overview of the sampling methodologies used (biotic and abiotic) and a short discussion on net efficiency is given in this introductory chapter.

1.5.1 Subtidal sampling

Demersal fishes and mobile macro-invertebrates are usually caught with a beam trawl, both for commercial and scientific purposes. The net mouth is kept open by a beam, carried by two triangular 'shoes', which run over the seabed. For catching the juvenile fauna a 3-m beam trawl was used (Fig. 1.5). One tickler chain and a chain in the ground rope of the net are attached between the runners to enlarge the net efficiency (see further). In most cases the beam trawl was equipped with a 6-m long small-meshed net, i.e. mesh-sizes of 5x5 mm (10 mm stretched) or 6x6 mm in the cod-end (the last 2 m of the net). During the earliest surveys (mainly in the Oosterschelde before 1986), a mesh-size of 10x10 mm has been used, as well.

Many sledge types have been designed to sample the larger 'planktonic' organisms immediately above the bottom. The post(larval) stages of both fishes and macrocrustaceans (together with the preferred prey of the juveniles), which live in the lowest metre of the water column, are most efficiently sampled with a hyperbenthic sledge. In the Westerschelde and Oosterschelde a simple device was used (Fig. 1.6), consisting of a metal frame (1 m width), mounted on gliders, with 2 fine-meshed nets

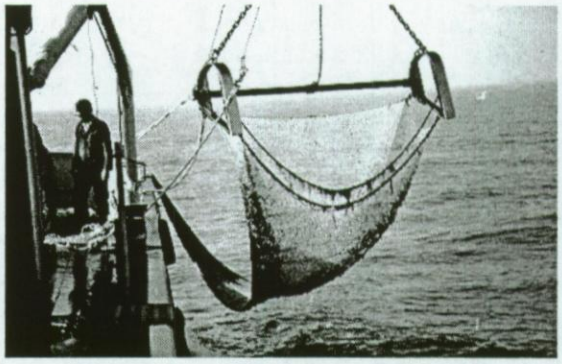

Fig. 1.5 A 3-m beam trawl with a small-meshed net, operated from the R.V. Luctor

(length 4 m, mesh 1x1 mm, total opening 0.8 m^2). More details on this sampling methodology and the hyperbenthic communities of the Westerschelde are given in Mees (1994).

The beam trawl and hyperbenthic sledge were operated from the RV Luctor (34 m, 500 Hp) from the Centre for Estuarine and Marine Ecology (CEME, Yerseke, NL). All samples in the subtidal habitat of the Westerschelde and Oosterschelde were taken at the border of the main channel at an average depth of 13 (± 3) m (range 7-21 m) below mean tidal level. Sampling was done with (in front of) the tidal currents, at a towing speed of approximately 2.3 m s^{-1} (4.5 knots) and over a distance of 1000 m per sample. Sometimes the distance was less to prevent clogging or tearing of the nets by storm-torn macrophytes, oysters or mud in the Oosterschelde, and mud or stones in the Westerschelde. All samples were taken during daytime except for the 24-hour cycle.

For completeness, it should be stated that several trials were made to sample upstream the Dutch-Belgian border with the beam trawl, but gear loss was so frequent (due to rubbish and ship wrecks) that no results can be reported. However, several researchers from the Laboratory for Aquatic Ecology (Catholic University Leuven) have been collecting fish and macro-crustaceans from the filtration devices in the cooling water intakes of several power-stations in the upper part of the estuary. More details on this sampling methodology and the fish community of the Zeeschelde are given in Maes (2000).

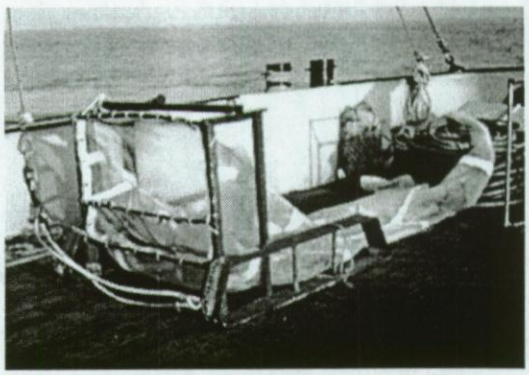

Fig. 1.6 A simple hyperbenthic sledge with two 1 mm^2 nets

1.5.2 Intertidal sampling

In the Westerschelde, the brackish intertidal sandflat of the Valkenisse-Ossenisse complex has been investigated by means of 2-m beam trawls. The lower intertidal (on average MTL –3 m) was sampled with the same 3-m beam trawl in the same way as in the subtidal. In the upper part of the intertidal (on average MTL –1 m), the fish and macro-crustaceans were sampled with a 2-m beam trawl, equipped with a small-meshed net (length 4m, mesh 5x5 mm) and 1 tickler chain. This sampling device was operated from the dinghy Riekus (7 m, CEME) at an average speed of 0.8 m s^{-1} (1.5 knots), over a distance of 800 m per sample. Sampling was limited to a 4-hour period around high tide.

On four intertidal flats in the Oosterschelde, samples were taken with a 2-m beam trawl. As these data were mainly used in a report so far (Hostens *et al.* 1994), no further details are given here.

The intertidal fish fauna from the Oosterschelde has been monitored for a number of years by means of 3 fyke nets (close to the dykes) and a weir or trap (near an intertidal flat). These are passive sampling techniques, where fykes are conical-shaped small-meshed nets, with a number of chambered one-way funnels, mounted on metal rings (Fig. 1.7). Traps work more or less the same way, but consist of a long 'leader' net (>100 m long) mounted on stakes, which guide the fish into one or two larger, fyke-like chambers. These samples were gathered by commercial fishermen, and initially worked out by Bureau Waardenburg (Culemborg, NL) (Meyer 1989).

A small stow net (length 5 m, opening 1 m^2, mesh 1 mm^2) mounted on a metal frame, has been operated from a bridge in several intertidal saltmarsh creeks in the brackish part of the Westerschelde (Fig. 1.8). This technique is comparable with fyke nets. The net was placed on the creek bottom against the tide to catch the migrating nekton fauna, and emptied every hour as long as water was present in the creeks. More details on this sampling device and the nursery/refuge function of the intertidal saltmarsh creeks are given in Cattrijsse (1994).

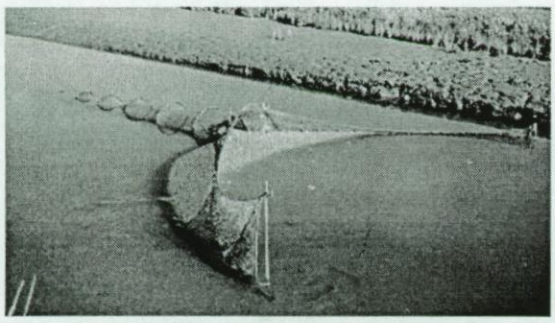

Fig. 1.7 A fyke net, used in the intertidal

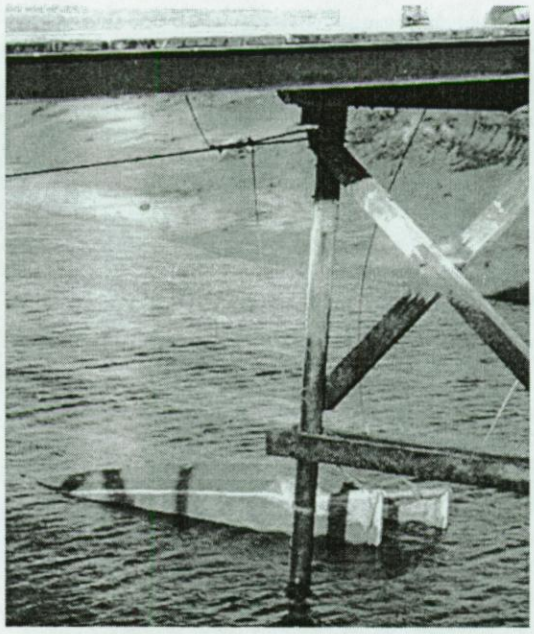

Fig. 1.8 A modified stow net, operated from a bridge in an intertidal saltmarsh creek

1.5.3 Net efficiency

The estimates of all population parameters are subject to various sources of bias. Net efficiency, or the proportion of fish caught in relation to the total available fish that can be caught, is a major source of uncertainty (Kjelson & Colby 1976). Few studies have assessed net efficiency thoroughly, as catch efficiency is dependent on the biotic component aimed at, the size and morphology of the target species, gear and habitat type, environmental conditions, manipulation of the sampling device, etc. (Hemingway & Elliott 2002). For most sampling devices net efficiency has never been investigated. Therefore, a net efficiency of 100 % is assumed for both the hyperbenthic sledge and the stow net (see Mees & Jones 1997 and Cattrijsse 1994 for more details).

On the other hand, beam trawls seem to have a low and variable net efficiency (Rozas & Minello 1997). Beam trawls are generally accepted to catch 20 to 33 % of the available fauna (Kuipers 1975, Elliott & Taylor 1989). Fish can escape from a beam trawl in four ways: through the meshes, underneath the ground rope, over the beam, and sideways (Kuipers 1975). Escapement through the meshes will be lower for larger individuals and for species with ornamental projections or spines (like most macrocrustaceans). On sandy bottoms, escapement under the gear can be limited by using one or more tickler chains. The tickler chain and the ground rope are longer than the beam to disturb the fishes and invertebrates before being covered by the net. Fast swimmers and larger fish can be expected to be able to avoid a small beam trawl by moving up or sideways (see Chapter 7-Add.).

In a number of surveys presented in this thesis, several parallel hauls were taken per sampling point (see further). Multivariate analyses always showed a high similarity between the 'replicate' samples, as they always clustered together (*e.g.* Hostens *et al.* 1993, Hostens *et al.* 1994, Verbeke 1994). This partly shows that the efficiency of a beam trawl does not vary much on sandy bottoms.

In conclusion, it is either impossible or too labour-intensive to calculate actual densities for every size of every species in every sample. The densities reported in this study are therefore to be considered as rough estimates. Although, a net efficiency of 20 % for all size classes of all fish and macro-invertebrates caught with a 3-m beam trawl, may be something of a wild guess, it is believed that it will give better population estimates, than assuming 100 % efficiency.

1.5.4 Environmental variables

Environmental information is important to explain the structure and function of biotic assemblages. Of course, the collection of a whole range of environmental data is expensive and time consuming. Salinity (psu), temperature (°C), dissolved oxygen (mg l^{-1}) and turbidity (m^{-1}) are believed to be the master controlling factors for fish assemblages (see Hemingway & Elliott 2002). The first 3 variables were measured approximately 1 m above the sea bottom with a CTD-sampler (Conductivity, Temperature, Depth). Turbidity was calculated as the reciprocal of secchi disc depth (light extinction). Moreover, sediment samples have been taken a few times in the different systems with a van Veen grab. The median grain size and silt concentration were measured with a Coulter LS Particle Size Analyser.

1.6 Overview of the available data and surveys

The present study is based on different large datasets, and several people have been working on part of the data. Table 1.2 gives an overview on all available data, though not all of them were used for the thesis. Some data were only published in reports, others were only used in the papers given as addenda. Most of the data have been used for several poster and oral presentations at international symposia and workshops. For completeness, information is given on the sampling of (post)larval fish and macro-crustaceans, and on the availability of environmental data. Most data were gathered by the Marine Biology Section of Ghent University (Belgium; before 1990 by O. Hamerlynck, after 1990 by K. Hostens for the 'epibenthic' data), in close cooperation with and with the logistic support of the Centre for Estuarine and Marine Ecology (CEME, Yerseke, the Netherlands), except the quarterly subtidal and the intertidal data of the Oosterschelde (gathered by CEME, NL; before 1990 under direction of R.H.D. Lambeck, after 1998 under direction of H. Hummel) and the fyke catches in the Oosterschelde (data gathered by Bureau Waardenburg, NL, and now property of CEME). Part of the 'epibenthic' data have been (re-)entered in the huge benthos database of the CEME. The length-frequency, density and biomass data on the demersal fish and macro-invertebrates, and the environmental data will be attached as a CD-rom.

At a number of occasions no samples could be taken, mostly due to bad weather conditions, sometimes due to logistic problems. As several people and institutes were involved in the numerous sampling campaigns, a few samples inevitably got lost, either completely or partly. Only a limited part of the epibenthic (sub)samples was taken to the lab (and is still available) for further analyses and/or determination. Computerization of the data was sometimes difficult, as surely for the earlier surveys (prior to 1989), only the notes taken aboard of the ship were available, which were not always accurate (*e.g.* subsampling conversions, mesh-size, identification uncertainties). See Fig. 1.3 for the different sampling locations.

1.6.1 Westerschelde

Subtidal beam trawl samples were taken during the following surveys:

1. monthly surveys were conducted along the salinity gradient at 14 subtidal locations between January 1988 and December 1991. Basic data were reported in Hostens *et al.* (1996) and partly in Puturuhu (1994)
2. this monitoring was repeated on a quarterly basis at the same 14 subtidal locations between September 1999 and May 2000. The number of sampling points was reduced to 8 for the period August 2000 - November 2001
3. a third series was limited to the brackish part of the Westerschelde, where two-monthly surveys at 4 subtidal locations (and some extra) were conducted in the period January - December 1990 (with 3 parallel hauls per location), and monthly surveys at the same 4 stations (but single hauls) in the period January - December 1991. Basic data were derived from Verbeke (1994)
4. a 24-hour cycle (actually 26 hours) has been carried out at subtidal station 12 on 18-19 September 1991, with samples taken every 2 hours. Basic data were derived from Muhando (1992).

Simultaneously, hyperbenthic sledge samples were taken in the subtidal. Several theses and papers on the hyperbenthic fauna from the Wester-

Table 1.2 Overview of the different available and used datasets and surveys

System Subhabitat/campaign	sampling device	period	frequency	# surveys	# locations	# samples	remarks	env. var.	Chapter
Westerschelde									
subtidal 'gradient'	3-m beam trawl	Jan88-Dec91	monthly	47	14	647		yes	all, except 4, 4add, 7add, 8
	hyperbenthic sledge	idem					larvae, prey		7, 8add, 9
subtidal 'brackish'	3-m beam trawl	Jan90-Dec90	2-monthly	5	4	60	3 hauls/loc	yes	7, 9
		Jan91-Dec91	monthly	11	4	44		yes	7, 9
subtidal '24h'	3-m beam trawl	Sep91	2-hourly	1	1	13		yes	8
	hyperbenthic sledge	idem					larvae, prey		8
subtidal 'gradient 2'	3-m beam trawl	Sep99-May00	quarterly	4	14	56		yes	5, 6, 8, 9
	hyperbenthic sledge	idem					larvae, prey		8
	3-m beam trawl	Aug00-Nov01	quarterly	6	8	47		yes	5
	hyperbenthic sledge	idem							
intertidal flat	3-m beam trawl	Mar92-Oct92	monthly	8	10	80	Valkenisse	yes	7, 9
	2-m beam trawl	idem		7	10	59	+Ossenisse	no	8, 9
intertidal saltmarsh	stow net	Mar90-Oct91	monthly	18	1		Saeftinghe	yes	9
		Apr99-Oct99		5	1		Idem	yes	9
		Mar90-Augt91		18	1		Waarde	yes	9
Oosterschelde									
subtidal 'whole'	3-m beam trawl	Jun83	once	1	36	29		no	9
		May84-Oct86	±quarterly	9	36	321	no winter	no	3, 9
		Feb87-Nov89	quarterly	12	36	430		no	3, 4, 5, 9
subtidal 'selected'	3-m beam trawl	Oct87-Nov88	fortnightly	26	3	229	3 hauls/loc	no	3, 9
		Nov88-Dec89	monthly	14	4	56	3 hauls/loc	limit	3add, 9
	hyperbenthic sledge	Dec88	once	1	4	4			
subtidal 'whole 2'	3-m beam trawl	Aug99-Nov01	quarterly	12	14	167	sedim. Feb00	yes	4, 5, 6add, 9
	hyperbenthic sledge	Idem					Postlarvae		9
Intertidal active	2-m beam trawl	Apr84-Nov84	fortnightly	13	4	489	10 hauls/loc	no	9
		May85-Oct85	fortnightly	10	3	273	10 hauls/loc	no	9
Intertidal passive	Fyke net + weir	79-88	fortnightly	216	4	860		no	3add, 9
Voordelta									
Subtidal 'whole'	3-m beam trawl	May88-Dec89	monthly	20	24	457	2 depths	yes	3, 3add, 4add, 7add
	hyperbenthic sledge	idem					Postlarvae		
Subtidal 'grevelingen'	3-m beam trawl	Oct92-Jul94	monthly	20	8	160	2 depths	yes	
	hyperbenthic sledge	idem							

schelde have been published (*e.g.* Mees *et al.* 1993a, Mees *et al.* 1993b, Mees *et al.* 1994, Mees & Jones 1997, Fockedey & Mees 1999). A paper on the post-larval fish from the Dutch Delta area was published by Beyst *et al.* (1999). The data on (post)larval fish and macro-invertebrates were derived from Mees (1994) and Chavatte (2001).

Intertidally, two different beam trawl surveys were performed on a large brackish sandflat. No hyperbenthic samples were taken here. Basic data were reported in Hostens *et al.* (1996):

1. monthly surveys were carried out between March and October 1992 at 10 locations in the lower intertidal with a 3-m beam trawl. Basic data were partly derived from Sas (1993)
2. simultaneously, the upper intertidal was sampled at 10 (and several extra) locations with a 2-m beam trawl.

In the intertidal saltmarsh creeks, monthly samples have been gathered with a stow net, during the periods March 1990 - October 1991 and April - October 1999 in the brackish saltmarsh 'Het Verdronken Land van Saeftinghe', and during the period March 1990 - August 1991 in the much smaller brackish saltmarsh 'Schor van Waarde'. Several theses and papers on the nekton fauna from intertidal saltmarsh have been published (*e.g.* Cattrijsse *et al.* 1994, Cattrijsse *et al.* 1997). The data on postlarval fish and macrocrustaceans were derived from Cattrijsse (1994) and Hampel *et al.* (in press).

1.6.2 Oosterschelde

Subtidally, the following beam trawl surveys have been conducted in the Oosterschelde:

1. more or less quarterly throughout the Oosterschelde (except the northern part) at 36 locations between June 1983 and November 1989. Basic data were reported in Hostens *et al.* (1993)
2. the monitoring was repeated on a quarterly basis, but limited to 12 locations, with additionally 2 locations in the northern part during the period August 1999 - November 2001. During these surveys, the hyperbenthic sledge was used simultaneously. Postlarval data were derived from Chavatte (2001)
3. fortnightly surveys were conducted between October 1987 and November 1988 at 3 locations, and at 4 locations (1 extra) from November 1988 to December 1989 on a monthly basis. The stations were located in the western and central part, with 3 parallel tows per station. Basic data were reported in Hostens & Hamerlynck (1993)

Intertidally, a 2-m beam trawl was used on 4 intertidal flats during fortnightly surveys in the period April - November 1984, and on 3 locations in the period May – October 1985. On each location 10 replicate hauls were taken. These data were reworked in Hostens *et al.* (1994).

Fyke catches in the Oosterschelde were taken on a fortnightly basis between 1979 and 1988 at 4 intertidal locations. These data have been reworked in Hamerlynck & Hostens (1991) and are presented in Chapter 3-Add.

1.6.3 Voordelta

In the Voordelta, 24 stations were sampled both with a 3-m beam trawl and a hyperbenthic sledge, covering two depth strata (MTL -5 m and MTL –10 m) at 12 localities in the ebb-tidal deltas of the Oosterschelde and the Grevelingen and in the more seaward area inbetween both deltas. The sampling was carried out on a monthly basis during the period May 1988 - December 1989. These data were partly gathered in order of Rijkswaterstaat (Ministry of public transport, NL), and have been reported in several reports, theses and papers. They formed the main basis of several papers given as addenda (Chapter 4-Add., Chapter 7-Add., Chapter 2-Add.2).

The surveys in the Grevelingen ebb-tidal delta (4 stations, 2 depths) were repeated during the period September 1992 – July 1994. These data were partly published in Arellano (1995) and Arellano *et al.* (1995), but were not used in the present thesis.

The papers included in the present thesis have been written over a timespan of 13 years. Several chapters only use part of the available data. Either the other data were not yet computerized at the moment of writing the specific chapter, or only shorter but similar sampling periods were investigated for comparative reasons. As shown in Table 1.2 the bulk of the thesis is based on the subtidal monitoring surveys in both the Westerschelde and the Oosterschelde during the periods 1988-'89 and 1999-2001. Most of the other sub- and intertidal surveys have been used in the papers on feeding ecology and in the final chapter.

1.7 Objectives of the thesis

The main aim of this study is to provide a baseline for future functional and process studies on the fish and macro-invertebrates of the Delta area, and of the Westerschelde and Oosterschelde estuaries in particular. The Westerschelde estuary is affected by high organic waste loads and by industrial pollution (Baeyens *et al.* 1998, Van Damme *et al.* 1999) the Oosterschelde by major engineering works during the past decades (Nienhuis & Smaal 1994b). To comply with international standards, a massive reduction of the pollution load of the Westerschelde will have to be achieved in the (near) future. Most probably, the Oosterschelde will be subject to hydraulic engineering interventions (*e.g.* freshwater input) in the future, as well. The impact assessment of these changes will hopefully be monitored. A baseline study is a prerequisite for such a monitoring program.

Although the different data sets were gathered through different projects - partly before the start of the thesis, others specifically designed for it - they all suit the same purpose: enlarging our knowledge on the nursery function of the Delta area for demersal fish and macro-invertebrate species. Estuaries, and more specifically fish and macro-invertebrates within these estuaries, have received considerable international attention during the last decades (see Elliott & Hemingway 2002). The thesis fits within several national and European projects on biology and ecology of 'benthic' organisms. Most of the work has been carried out at the Marine Biology Laboratory (UGent), but the thesis would not have been possible without the logistic support from, and scientific cooperation with the Centre of Estuarine and Marine Ecology (CEME, Yerseke, the Netherlands).

To assess the nursery function, information is needed on (changes in) larval and postlarval recruitment, habitat complexity and availability, environmental properties and prey availability. The thesis benefits from complementary research on other biotic and abiotic compartments in the Delta area. Geomorphology, physics, chemistry, organic material, bacteria, phytoplankton, zooplankton, hyperbenthos, mi-

crophytobenthos, meiobenthos, macrobenthos, and birds were studied in detail, both in the Westerschelde and the Oosterschelde. In the Marine Biology Section of Ghent University, the hyperbenthos of the Westerschelde has been thoroughly studied by Mees (1994), and more recently of the Oosterschelde by Chavatte (2001), while the nekton from intertidal saltmarsh creeks was studied by Cattrijsse (1994). General reviews on the environmental and ecological properties are given in Meire & Vincx (1993), Heip & Herman (1995), and Van Damme *et al.* (1999) for the Westerschelde, and in Nienhuis & Smaal (1994a) and van Berchum & Wattel (1997) for the Oosterschelde.

Some of the advantages of using fish and macro-invertebrates as biological indicators are: (1) they can easily be identified in the field; (2) they have a well-known biology and ecology; (3) they may indicate changes in other ecosystem compartments, as they are major contributors in the trophic food chain (Marchand *et al.* 2002). Still, it may be difficult to differentiate natural changes (mainly yearly variability) from those caused by humans (Wolfe *et al.* 1987). Estuaries are complex ecosystems with many natural disturbances, induced by hydroclimatic changes. On the other hand, estuaries have been under human pressure during their whole evolution, and ecological studies suffer from the fact that data from pristine times are almost non-existent (Marchand *et al.* 2002).

To provide a baseline for the understanding of the nursery function, both structural and functional patterns have to be investigated. The specific objectives of this thesis are:

1. to describe the spatial and temporal patterns in diversity, density, biomass and growth of the demersal fish and macro-invertebrates in the Westerschelde and Oosterschelde estuaries, and to evaluate the relation with the major structuring environmental variables

2. to describe the structural patterns at several temporal scales, i.e. short-, mid-, and long-term changes, and at several spatial scales, i.e. within and between estuaries and subhabitats in these estuaries

3. to evaluate the abiotic and biotic influences (including human impact) at the community level, and to predict distribution patterns at the species level, in both estuaries

4. to study the temporal and spatial differences in trophic niche and feeding patterns of several fish and macro-invertebrates in the Westerschelde estuary

5. to evaluate the importance of hyperbenthic organisms, and in particular mysids, in the food web of the Westerschelde estuary.

1.8 Outline of the thesis

In this ecological thesis, the aim is to understand the interaction between the organisms and between the organisms and their environment. Most chapters have been or will be published as such in the international literature. Rather for completeness than as part of the thesis, most chapters are supplemented with an addendum, i.e. papers with complementary information to the Westerschelde and Oosterschelde estuaries that were published as such. My contributions to the papers where I am not the first author are computerization of the data from the field data sheets, data analysis and stomach content analysis.

The **structural patterns** in the fish and macro-invertebrate assemblages, both in space and in time, are described in **PART I** (chapters 2 through 6). The spatial and short-term temporal patterns along the salinity gradient in the subtidal Westerschelde are described in **chapter 2** based on the monthly data of 1988-'89, and in an addendum based on the monthly data of 1990. In a second addendum, an important paper on the strength of multivariate techniques is given, based on monthly data from 1989 from the Oosterschelde, the Westerschelde and the Voordelta:

***Hostens K** (2000) Spatial patterns and seasonality in the epibenthic communities of the Westerschelde (Southern Bight of the North Sea). J Mar Biol Ass UK 80: 27-36*

***Hostens K** (1996) Spatial and temporal patterns in the epibenthos of the Westerschelde. Prog Belg Oceanog Res 107-110*

*Hamerlynck O, **Hostens K**, Arellano RV, Mees J, van Damme PA (1993) The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands): spatial structure. Neth J Aquat Ecol 27(2-4): 343-358*

In **chapter 3** the spatial and mid-term patterns in the fish assemblages of the Oosterschelde are based on the subtidal data, sampled fortnightly in 1988 (in comparison to the Westerschelde and Voordelta), and on quarterly samples in the periods 1988-'89 and 1984-'85. Its twin paper, based on intertidal data gathered with fykes between 1979-1988, is given in an addendum:

***Hostens K**, Hamerlynck O (1994) The mobile epifauna of soft bottoms in the subtidal Ooster-*

schelde estuary: structure, function and impact of the storm-surge barrier. Hydrobiologia 282/283: 479-496

Hamerlynck O, ***Hostens K*** *(1994) Changes in the fish fauna of the Oosterschelde - a ten year time series of fyke catches. Hydrobiologia 282/283: 497-507*

In **Chapter 4** long-term patterns in the fish fauna of the Oosterschelde are presented, based on quarterly data from 1987-'89 and 1999-2001. This chapter deals with the possible effects of the Deltaworks in the Oosterschelde. In an addendum, the consequences of the civil engineering works in the ebb-tidal Delta of the Grevelingen were evaluated:

Hostens K*, Hummel H, Mees J, Vincx M, Heip CH (submitted a) The fish fauna of the Oosterschelde, a decade after completion of the engineering works. J Sea Res*

Hamerlynck O, ***Hostens K****, Mees J, Arellano RV, Cattrijsse A, van de Vyver P, Craeymeersch JA (1992) The ebb-tidal delta of the Grevelingen: a man-made nursery for flatfish? Neth J Sea Res 30: 191-200*

Chapter 5 gives detailed short- and long-term patterns for several macro-invertebrates in a comparison between the two estuaries, based on quarterly data from 1988-'89 and 1999-2001:

Hostens K*, Mees J, Hummel H (submitted b) The mobile macro-invertebrate fauna of the Oosterschelde and the Westerschelde (SW Netherlands). J Mar Biol Ass UK*

In **Chapter 6** it is tried to predict both fish and macro-crustacean presence and density in relation to the Westerschelde environment at the species level. Most data from the subtidal 'gradient' surveys (1988-'91 and 1999-2001) are used. In the addendum, these models were applied to a limited dataset from the Oosterschelde:

Hostens K *(submitted) Fish and macro-crustacean response surfaces to environmental gradients in the Westerschelde estuary. Mar Ecol Prog Ser*

Hostens K *(unpubl. data) Application of the Westerschelde response models to fish and macro-crustacean data from the Oosterschelde*

The **functioning** of the different habitats in the Dutch Delta area as nurseries for juvenile fish and macro-crustaceans is evaluated in **PART II** (chapters 7 and 8). Data from different sub- and intertidal surveys were used. Both chapters are mainly focused on the Westerschelde, and emphasize the (underestimated) role of hyperbenthic prey – and particular mysids – for the higher trophic levels of the estuarine food web.

In **Chapter 7** the importance of mysids in the diet of several fish species in the Westerschelde is shown. A paper on the feeding ecology of two gadoid species in the Voordelta is given as addendum:

Hostens K*, Mees J (1999) The mysid-feeding guild of demersal fishes in the brackish zone of the Westerschelde estuary. J Fish Biol 55: 704-719*

Hamerlynck O, ***Hostens K*** *(1993) Growth, feeding, production and consumption in O-group bib Trisopterus luscus L. and whiting Merlangius merlangus L. in a shallow coastal area of the SW Netherlands. ICES J Mar Sci 50: 81-91*

Diurnal, seasonal and spatial patterns in the diet of the brown shrimp in the Westerschelde are discussed in **Chapter 8**. In an addendum, a basic paper on the food webs of the Westerschelde is included:

Hostens K, *Mees J (submitted) The diet of brown shrimp Crangon crangon (L.) in the Westerschelde estuary. Mar Biol*

Hamerlynck O, Mees J, Craeymeersch JA, Soetaert K, ***Hostens K****, Cattrijsse A, van Damme PA (1993) The Westerschelde estuary: two food webs and a nutrient rich desert. Prog Belg Oceanog Res 217-234*

Finally, in **Chapter 9** an overview is given on the nursery function of both the Westerschelde and the Oosterschelde estuaries. All sub- and intertidal datasets on the juvenile and postlarval life stages are used. The demersal fish and macro-invertebrate species are categorised by means of different functional ecotrophic guilds. This forms the basis of a two-dimensional foodweb in the Westerschelde:

Hostens K *The demersal fish and macro-invertebrate assemblages of the Westerschelde and Oosterschelde estuaries: overview and final conclusions.*

CHAPTER 2 SPATIAL PATTERNS AND SEASONALITY IN THE EPIBENTHIC COMMUNITIES OF THE WESTERSCHELDE (SOUTHERN BIGHT OF THE NORTH SEA)

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Key words: estuary, demersal fish, epibenthic macro-invertebrates, *Crangon crangon*

Published in *Journal of the Marine Biological Association of the U.K. 2000, 80: 27-36*

Abstract. *Beam trawl samples were taken monthly between January 1988 and December 1989 in 14 subtidal stations along the longitudinal axis of the Westerschelde estuary. The estuary harboured high densities of epibenthic species (total average of 2250 ind 1000m^{-2}). Only 37 fish species were recorded and three mobile macro-invertebrate species were quantified. Seventeen epibenthic species were common, only eight of which were very abundant. An overall dominance of the brown shrimp Crangon crangon was noted. The near absence of anadromous and freshwater species was correlated with the low oxygen concentrations upstream the Dutch-Belgian border. The epibenthic species could be divided into a polyhaline and a mesohaline community along the main salinity-oxygen-turbidity gradients of the estuary. The mesohaline zone was characterized by higher densities and biomasses for shrimps, gobies and flatfishes. The spatial structure in the epibenthic community of the polyhaline zone was more influenced by the watermasses from the sea and inflowing channels, and was correlated with the degree of exposure (current velocities and tides). A classification is proposed, based on the season in which the epibenthic species occur in the estuary, and on their life stages and abundances during that period. The monthly data demonstrate that while the eight abundant epibenthic species were generally present throughout the year (summer or winter resident), the majority tended to appear in the Westerschelde at varying times (summer, winter or bimodal) and often remained in large numbers (nine common species) for only a short time. The fact that mainly juveniles were recorded in the higher density classes, suggests that the Westerschelde estuary still acts as a nursery area for many epibenthic species.*

2.1 Introduction

The Westerschelde estuary is the maritime zone of the river Schelde in the Delta area of the Netherlands. It stretches from Vlissingen near the mouth to the Dutch-Belgian border (Fig. 2.1). This part of the estuary is characterized by large intertidal sandflats and two main subtidal channels (mud percentage lower than 2%), and it is bordered by mudflats and saltmarshes (Van Maldegem *et al.* 1993). The tidal zone upstream the border is called the Zeeschelde. The Schelde is a highly polluted system, both with industrial and domestic waste. It is especially threatened by huge organic loads, but it also suffers from strong anthropogenic perturbations such as dredging, dumping, sand extraction, land reclamation, and - to a lesser extent – recreation and industrial fisheries.

De Veen *et al.* (1979) reported on a 10 year survey on some economically important epibenthic species in the Westerschelde. These authors compared the system with the Wadden Sea and the Dutch coastal zone, and emphasized its importance as a

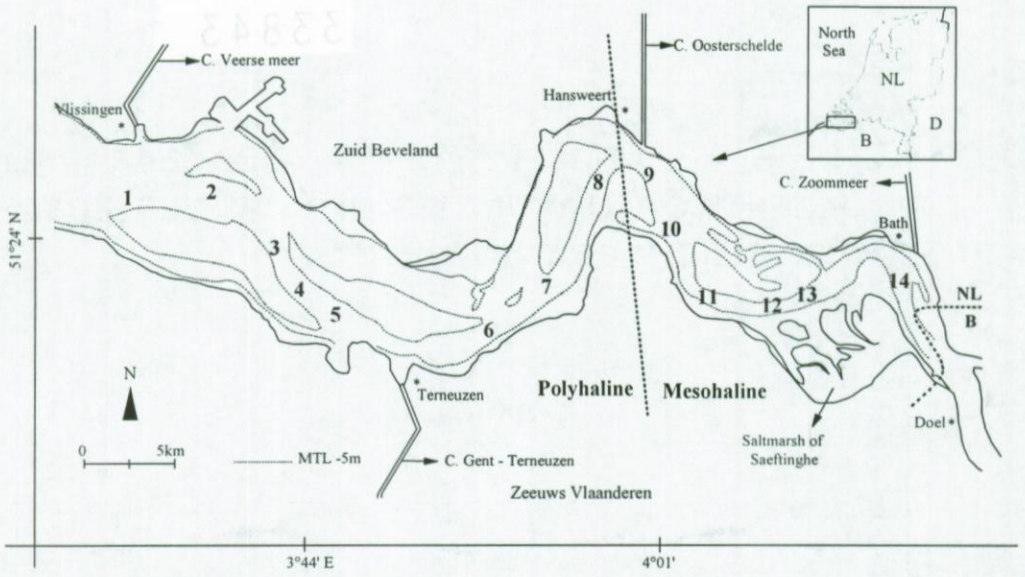

Fig. 2.1 Map of the study area with location of the 14 sampled stations in the subtidal of the Westerschelde. Note the division between the 'polyhaline' and 'mesohaline' epibenthic communities around Hansweert

nursery area. In Chapter 2-Add.2 the fish fauna of the Westerschelde was compared with that of the neighbouring Oosterschelde. Data on the fish fauna of the lower Zeeschelde were presented by Van Damme *et al.* (1994). The present study focuses on the abundance and distribution of the demersal fishes and mobile macro-invertebrates, which together constitute the epibenthic community. Fish distribution and abundance in estuarine and coastal environments are determined by physical and chemical factors (*e.g* salinity, temperature, water transparency, tidal cycles, wave action and wind), and biotic factors (*e.g* migration, reproduction, feeding and habitat selection) (Morin *et al.* 1992). The spatial and seasonal distribution patterns of the epibenthic species are described by means of multivariate statistical techniques, and are correlated with some environmental variables. A classification of the epibenthic species is proposed in accordance with their presence in the estuary.

2.2 Material and methods

Between January 1988 and December 1989 monthly samples were taken at 14 subtidal stations, following the 10 m depth contour along the longitudinal axis of the Westerschelde. The stations were more or less evenly distributed between 3 and 52 km upstream from Vlissingen (Fig. 2.1). The epibenthos was always sampled during daytime with a 3-m beam trawl, which was towed over a distance of 1000 m from the RV 'Luctor' (34 m, 500 pK). The beam trawl was equipped with a small-meshed net (10 mm stretched in the codend), one tickler chain and a chain in the groundrope. After sampling, four environmental variables were measured: temperature (°C), salinity (psu), dissolved oxygen content (mg l^{-1}) and Secchi disc depth (cm). The latter was reciprocally transformed, thus becoming a measure of turbidity (light extinction, cm^{-1}).

All fish were identified to species level and measured to total length on board, except for the gobies which were identified and measured to standard length in the laboratory. Only the most abundant and conspicuous mobile macro-invertebrates (*Crangon crangon* and two crab species) were counted and/or weighed in bulk. A number of rare invertebrate species could not be quantified. From hyperbenthic studies in the subtidal of the Westerschelde (Mees *et al.* 1993b), we know that the prawn species *Palaemonetes varians* and *Palaemon elegans*, the crabs *Portumnus latipes* and *Eriocheir sinensis*, and the hermit crab *Pagurus bernhardus* are sometimes present in low numbers. Density values are expressed in numbers of individuals per 1000 m^2, assuming a netefficiency of 20 % for the 0- and 1-groups of all fishes and invertebrates (Chapter 3). The biomass was calculated from the length-frequency tables, by means of length-weight regressions, which were based on measurements in the Oosterschelde and the Voordelta area (see Tables 4.2 and 5.2). Biomass is expressed in grams Ashfree Dry Weight (ADW) per 1000 m^2.

Different multivariate techniques were used to describe the spatial and seasonal community structure of the epibenthos, based on the average density and biomass per station and per month over the period 1988-89. Prior to the multivariate analyses, the data were fourth-root transformed. Different data reductions were based on average density and biomass levels for the whole study period, excluding the rare species. Also the environmental variables were

Table 2.1 Average density (ind $1000m^{-2}$) and biomass (gADW $1000m^{-2}$) over the period January 1988 - December 1989, for the whole epibenthic community (fish and invertebrates) and for the fish alone, per station (25 campaigns) and per month (28 locations)

	Polyhaline								Mesohaline					
Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Km from mouth	3	8	11	13	16	23	26	30	34	36	40	43	47	52
Total density	1900	2220	1370	1490	1000	1390	1250	1650	2390	4440	4130	2810	1950	3310
Fish density	170	320	90	200	150	160	250	300	450	1070	750	330	220	770
Total biomass	1000	610	500	580	480	480	430	500	970	2430	1880	940	790	1860
Fish biomass	320	130	120	220	200	160	180	180	500	1630	1080	340	370	1280

	Winter			Summer						Winter		
Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fish density	700	210	130	270	130	120	470	440	840	510	320	320
Total biomass	2110	560	440	660	510	570	1050	860	1430	1200	1200	1110
Fish biomass	1810	450	320	520	180	140	170	170	420	530	480	760

averaged per station and per month. Two Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979) and Group Average Sorting cluster analysis based on the Bray-Curtis dissimilarities (Bray & Curtis 1957), were used as classification techniques.

The ordination techniques used were Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) (Jongman *et al.* 1987). (also see §9.6.1). As the different techniques applied to both density and biomass data yielded similar results, only the cluster analysis and the CCA with the average biomass data per station (criterion: total average density > 0.1 ind $1000m^{-2}$) and the CCA with the average biomass data per month (criterion: total average density > 0.01 ind $1000m^{-2}$), are presented.

Seasonality in the data was further analysed by means of some aspects of the biology of the epibenthic species. The period of maximum abundance and the modal length class during this period were extracted from the average density data and the length-frequency distributions per month. For *Crangon crangon* the patterns are based on biomass data, since this species was only weighed in bulk. No data on the densities of the different life stages of the invertebrate species were available. The epibenthic species were divided into different density classes and categories, depending on their seasonal occurrence and the time they spent in the estuary.

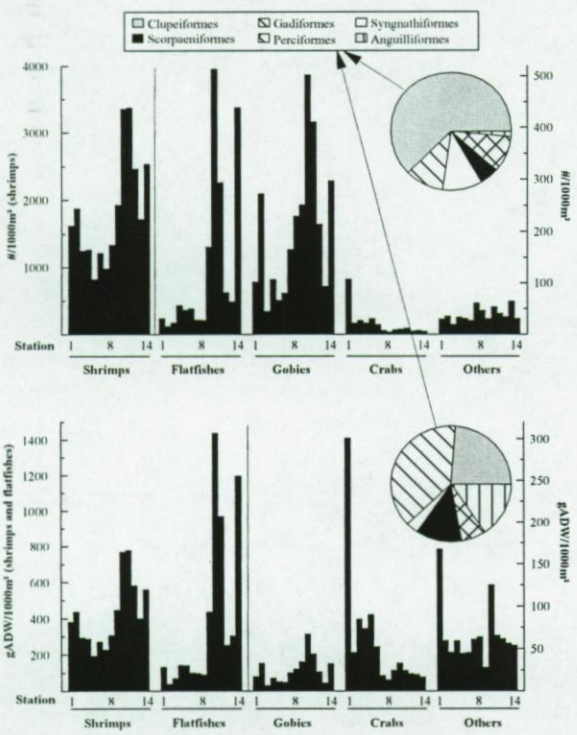

Fig. 2.2 Average density (ind $1000m^{-2}$) and average biomass (gADW $1000m^{-2}$) per station for the main epibenthic groups. The insets show the relative composition (averaged over all samples) of the 'Others' group. Note that the left axis only refers to "shrimps" in the density plot and to "shrimps" and "flatfishes" in the biomass plot

2.3 Results

2.3.1 Spatial patterns

During the study period a total of 37 fish and 3 invertebrate species were recorded: on average 8 and 11 species were caught per month and per station, respectively. The total average density for all stations over the period 1988-89 was 2250 ind $1000m^{-2}$ and the total average biomass amounted to 970 gADW $1000m^{-2}$. The brown shrimp *Crangon crangon* constituted some 80 % of the total density (Table 2.1).

Moreover, this species dominated the fauna along the entire salinity gradient sampled. Only in the more brackish stations (upstream of Hansweert) did the bigger flatfishes attain some higher biomass values (1440 gADW $1000m^{-2}$ at station 10) (Fig. 2.2). The third important group were the gobiid fish. In terms of density they were equally important as the flatfish (on average 200 ind $1000m^{-2}$). All three

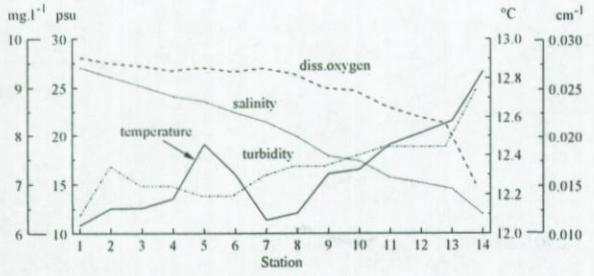

Fig. 2.3 Average values for the four environmental variables per station: dissolved oxygen (mg l^{-1}), salinity (psu), temperature (°C) and turbidity (cm^{-1})

groups showed similar density patterns along the salinity gradient: densities stayed uniformly low in the marine part (except for station 2) up till Hansweert; they then gradually increased in the brackish reaches and decreased again, but peaking again with very high densities in the last station around Bath (Fig. 2.2).

Two other groups did not follow this pattern: brachyuran crabs had higher biomasses in the marine part, and the group of all other fish species together had comparable values in all stations. The relative composition of this last group is given in the insets of Fig. 2.2. The clupeoids were most important in terms of density, while gadoids, Scorpaeniformes and eels had comparable biomass values.

The average values of the four environmental variables are presented in Fig. 2.3. Salinity gradually decreased from 28 to 12 psu upstream. The dissolved oxygen concentration remained above the saturation level downstream of Hansweert, decreasing to 8.2 mg l^{-1} with a decline to 7 mg l^{-1} at Bath. Turbidity showed the inverse pattern of the oxygen content. Temperature gradually increased in upstream direction from 12 to 13 °C, with somewhat higher values around stations 5 and 6.

Cluster analysis classified the 14 stations in two main groups, one upstream and the other downstream of Hansweert (Fig. 2.5). All stations were rather similar, with a maximum dissimilarity of 0.3 on a scale from 0 to 1. The CCA on the reduced biomass matrix visualizes the major gradients in the estuary and the environmental preferences of the main species. The four variables explain 73 % of the variance along the first axis (eigenvalue 0.09) (Fig. 2.4). The projection of the Cluster groups on the CCA plot shows that the more saline stations are separated from the more brackish (and turbid) stations. Two smaller clusters are suggested: stations 3-5, with shore crab *Carcinus maenas* and whiting *Merlangius merlangus* as characteristic species; and stations 10-13, characterized by high biomass values for sand goby *Pomatoschistus minutus*, the flatfish *Limanda limanda* and *Solea solea*, and herring *Clupea harengus*. Stations 6, 8 and 9 take up a position between these two groups; the dominant species are lozano's goby *Pomatoschistus lozanoi* and sea-snail

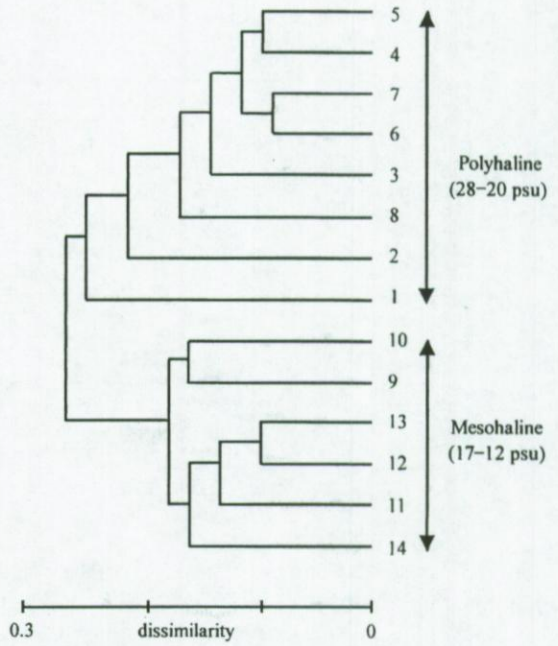

Fig. 2.5 Dendrogram of the cluster analysis, with an indication of the two zones and the degree of dissimilarity on a scale of 0-1

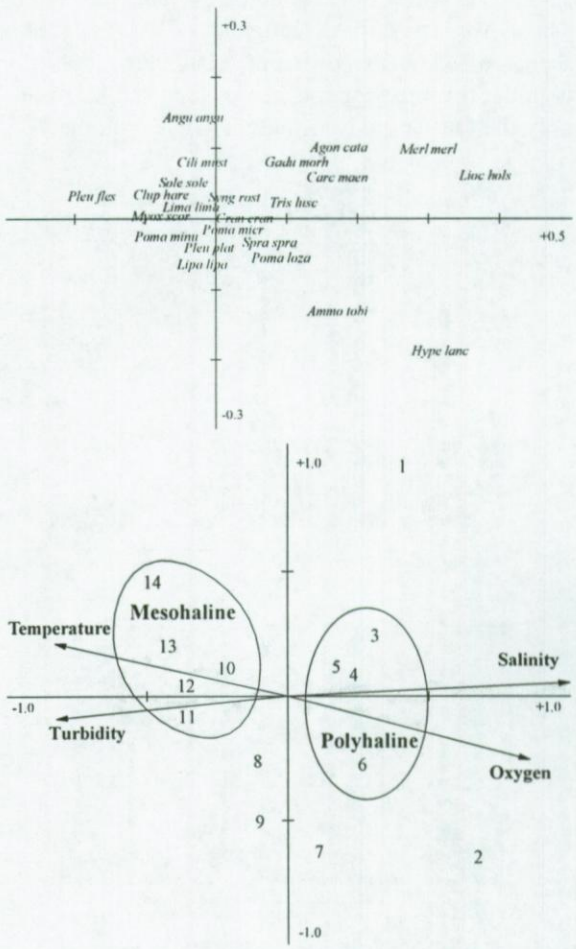

Fig. 2.4 CCA ordination plots (first two axes), based on a reduced set of the average biomass data and on the environmental variables per station, with a projection of the two main clusters. See **Table 2.2** for full species names (abbreviated to first 4 letters of genus and species names)

Table 2.2 Some biological aspects of the 40 epibenthic species caught in the Westerschelde, based on the monthly average densities over the period January 1988 - December 1989, with an indication of the proposed classifications

Abundancy class	Species	Systematic group	Density†	Period max. abundance	Month of, and max. abundance†	Seasonal class	Modal length class during period of max.‡	Main life stage	Life history
	Crangon crangon	Caridea	416.9	Jul–Nov	Sep, 939	Summer-resident		Independent	Marine
	Pomatoschistus lozanoi	Gobiidae	110.5	Aug–Oct	Sep, 529	Summer-resident	30–40	Juvenile	Brackish
	Limanda limanda	Pleuronectiformes	84.4	Oct–Jan, Jan	Jan, 385	Winter	60–90, 140–160	Juvenile	Marine
Abundant	*Pomatoschistus minutus*	Gobiidae	76.7	Jul–Sep	Jul, 344	Summer-resident	25–45	Juvenile	Brackish
	Solea solea	Pleuronectiformes	33.4	Jan–Apr	Apr, 215	Winter-resident	90–110	Juvenile	Brackish
	Sprattus sprattus	Clupeiformes	17.2	Dec–Jan, Jul	Jan, 53	Bimodal	65–80, 45	Juvenile	Marine
	Pleuronectes platessa	Pleuronectiformes	16.9	Sep–Feb	Jan, 70	Winter	70–100	Juvenile	Marine
	Carcinus maenas	Brachyura	16.6	May–Aug	May, 28	Summer-resident		Independent	Brackish
	Clupea harengus	Clupeiformes	7.7	Jan–Feb, Jul–Aug	Jan, 32	Bimodal	90–100, 45–55	Juvenile	Marine
	Pomatoschistus microps	Gobiidae	6.5	Nov–Mar	Jan, 24	Winter	30–40	Elder	Brackish
	Liocarcinus holsatus	Brachyura	4.1	May–Sep	May, 12	Summer		Independent	Marine
	Syngnathus rostellatus	Syngnathiformes	3.9	Aug–Sep, Jun	Aug, 10	Summer	90–100, 110–120	Juvenile	Marine
Common	*Ammodytes tobianus*	Perciformes	3.5	Feb–Apr	Apr, 9	Winter-resident	80–90	Junveile	Marine
	Pleuronectes flesus	Pleuronectiformes	2.7	Dec–Mar	Mar, 5.8	Winter-resident	200–400, 100–120	Independent	Catadromous
	Trisopterus luscus	Gadiformes	2.0	Jun–Aug	Jun, 9	Summer	70–75, (50–130∫)	Juvenile	Marine
	Merlangius merlangus	Gadiformes	1.3	Jun–Jul	Jun, 9	Summer	70–90	Juvenile	Marine
	Agonus cataphractus	Scorpaeniformes	1.0	Dec–Feb*	Jan, 2.6	Winter-resident	65–75	Juvenile	Marine
	Liparis liparis	Scorpaeniformes	0.8	May–Jul, Sep–Dec	Jun, 2.2	Bimodal	60–70, 110–120	Independent	Brackish
	Gadus morhua	Gadiformes	0.4	Sep–Nov*	Sep, 1.2	Summer	160–220	Elder	Marine
	Anguilla anguilla	Anguilliformes	0.3	May–Jul	Jul, 1	Summer	300–400	Elder	Catadromous
	Myoxocephalus scorpius	Scorpaeniformes	0.3	Feb–Mar	Feb, 1	Winter	160–200	Elder	Marine
	Hyperoplus lanceolatus	Perciformes	0.2	Jun–Sep	Jun, 0.7	Summer	150–180	Juvenile	Marine
	Ciliata mustela	Gadiformes	0.2	Sep–Nov	Oct, 1.3	Winter	100–120	Juvenile	Marine
	Gasterosteus aculeatus	Gasterosteiformes	0.2	Dec–Mar	Mar, 0.7	Winter	45–55	Juvenile	Brackish
	Zoarces viviparus	Perciformes	0.08	—	May, 0.2	Summer-resident	150–155	Juvenile	Brackish
	Trigla lucerna	Scorpaeniformes	0.06	May, Oct	Oct, 0.3	Bimodal	150–170, 45–60	Independent	Marine
	Mugilidae sp.	Perciformes	0.05	Oct–Dec	Oct, 0.3	Winter	40–45	Juvenile	Catadromous
	Engraulis encrasicolus	Clupeiformes	0.04	Sep–Oct	Oct, 0.3	Winter	65–75	Juvenile	Brackish
Occasional	*Syngnathus acus*	Syngnathiformes	0.04	Jun–Jul	Jul, 0.1	Summer	320–380	Elder	Marine
	Dicentrarchus labrax	Perciformes	0.04	Dec–Mar	Dec, 0.4	Winter	70–75	Juvenile	Brackish
	Pungitius pungitius	Gasterosteiformes	0.03	Mar*	Mar, 0.3	Winter	40–45	Juvenile	Fresh
	Alosa fallax	Clupeiformes	0.02	Nov**	Nov, 0.2	Winter	95–100	Juvenile	Anadromous
	Aphia minuta	Gobiidae	0.02	Apr–Jul	Oct, 0.06	Summer	40–50	Elder	Marine
	Scophthalmus rhombus	Pleuronectiformes	0.02	Jan–Apr	Sep, 0.07	Winter	200–300	Elder	Marine
	Lampetra fluviatilis	Petromyzontiformes	0.01	Jun**	Jun, 0.1	Summer	170–175	Elder	Anadromous
	Atherina presbyter	Atheriniformes	0.01	Sep–Oct**	Oct, 0.07	Winter	85–90	Elder	Marine
	Trachurus trachurus	Perciformes	0.01	Aug–Sep	Sep, 0.07	Summer	60–70	Juvenile	Marine
	Buglossidium luteum	Pleuronectiformes	0.006	May*	May, 0.07	Summer	55–60	Juvenile	Marine
	Pomatoschistus pictus	Gobiidae	0.006	Oct**	Oct, 0.07	Winter	30–35	Juvenile	Marine
	Solea lascaris	Pleuronectiformes	0.006	Jul**	Jul, 0.07	Summer	100–105	Juvenile	Marine

*, mainly 1988; **, mainly 1989; †, average density (ind 1000 m^{-2}) except for *Crangon crangon*, biomass (g ADW 1000 m^{-2}); ‡, total length (mm) except for Gobiidae, standard length (mm); ∫, range over the three months.

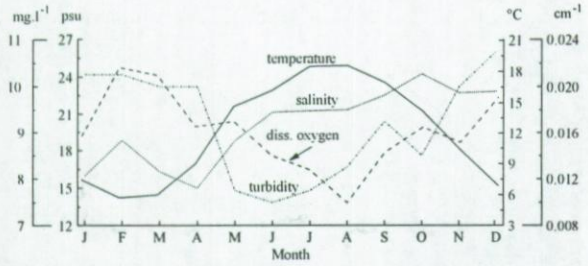

Fig. 2.6 Average values for the four environmental variables per month: dissolved oxygen (mg l^{-1}), salinity (psu), temperature (°C) and turbidity (cm^{-1})

Liparis liparis. Along the second axis (eigenvalue 0.02) stations 1, 2 and 7 are plotted near the edges. Stations 2 and 7 are characterized by Ammodytidae (*Ammodytes tobianus* and *Hyperoplus lanceolatus*).

2.3.2 Seasonality

Although most epibenthic species were caught throughout the year, their densities and biomasses displayed seasonal trends. Based on the period(s) of maximum abundance, the epibenthos could be divided into five categories. The 'resident species' were present in the estuary throughout the year (though not necessarily during their whole life history), and showed peak densities either in summer (summer-resident, SR) or in winter (winter-resident, WR). The 'bimodal species' (B) clearly showed two density peaks, while other species were almost exclusively present in the estuary during summer (summer-species, S) or during winter (winter-species, W). 'Summer' is defined as the period from May to September; 'winter' as October to April. Based on the average density over the period 1988-89 and on the modal length-classes, the epibenthos could further be divided into 6 density - life history groups. The species were classified as either occasional (O), common (C) or abundant (A), and as juvenile (J), elder (E) or life stage independent (I).

A total of 25 juvenile, nine elder and six independent species were found (Table 2.2). In the 'abundant' (8 species) and 'common' (9 species) density classes, mainly 'juveniles' were registered, while 'juvenile' and 'elder' species were more or less equally distributed over the 'occasional' density classes with less than 1 ind $1000m^{-2}$ (23 species). The numbers of 'summer' and 'winter' species were almost equal, namely 5 SR, 13 S, 4 WR and 14 W, but the distribution of the main life stages was different: 7 J, 5 E and 1 I in summer versus 10 J and 4 E in winter, and 6 J and 3 I in the group of resident species. The 4 'bimodal' species were either 'juveniles' or the two peaks were found to belong to two different cohorts, with the highest densities being recorded in the winter period (Table 2.2).

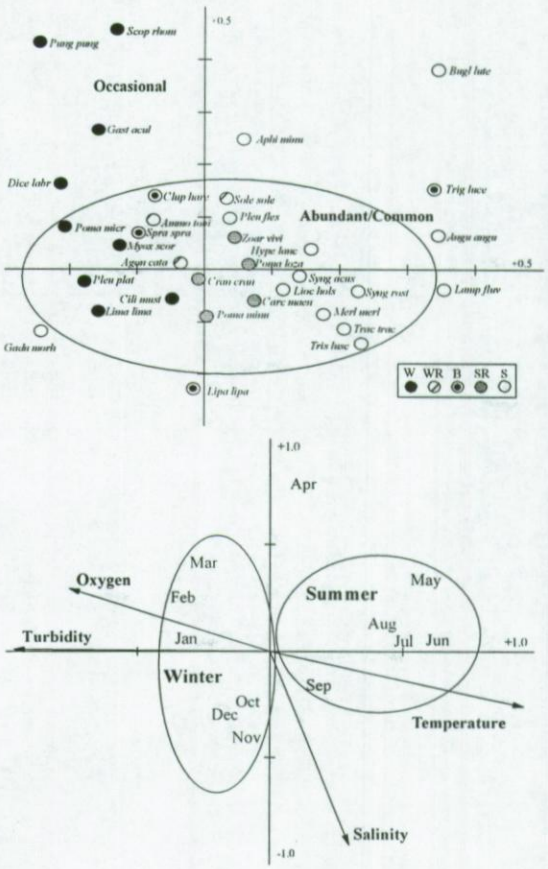

Fig. 2.7 CCA ordination plots based on the average biomass data and on the four environmental variables per month, with a projection of the proposed classification of the epibenthic species. See Table 2.2 for full species names (abbreviated to the first 4 letters of genus and species names). W, winter; WR, winter-resident; B, bimodal; SR, summer-resident; S, summer species

The seasonal patterns for the 4 environmental variables are presented in Fig. 2.6. The dissolved oxygen concentration gradually decreased from 10.5 mg l^{-1} in February to 7.5 mg l^{-1} in August. Temperature showed the inverse pattern with a minimum of 6 °C in February and a maximum of 19 °C in August. Turbidity was highest during the winter months (0.02 cm^{-1} from November to April), and dropped to a value of 0.01 cm^{-1} between May and July. Salinity increased from 16 in January to 23 in December, with an exception for March and April when low salinities of 15 were recorded.

The classification of the epibenthic species is reflected in the CCA plot of average biomasses per month (Fig. 2.7). The species-environment relations of the first two axes explain 92 % of the variance in the data. The 'winter' and 'summer' periods (as defined above) were separated along the first axis (eigenvalue 0.16). The 'winter' period could further be divided in 'early winter' (September - December) and 'late winter' (January - March) along the second axis (eigenvalue 0.07). The division in winter and summer species is in agreement with the plot of the months. Resident (R) species and common juvenile (C,J) and independent (C,I) species are mostly located near the

centre of the species plot. Occasional juvenile (O,J) and elder (O,E) species are plotted near the edges.

2.4 Discussion

2.4.1 Spatial distribution

The most abundant fish in estuaries are benthic or demersal species. The average densities for the most common species are comparable with those recorded by De Veen *et al.* (1979) for the period 1969-78 in Zeeland, and with those recorded for the Oosterschelde in 1988 (Chapter 3). In the Forth estuary maximum abundances for dab and plaice were lower, while these for whiting, clupeoids and eelpout were higher (Elliott *et al.* 1990). A beam trawl with a small-meshed net is very efficient for catching mobile macro-invertebrates, such as shrimps, crabs and echinoderms. These invertebrates generally are the main component of the demersal epibenthic communities in estuaries (80 % shrimp) and coastal zones (50 % starfish, 30 % shrimp) (Chapter 2-Add.2). Unfortunately, only the three most common macro-invertebrate species could be quantified. This has no implications for the structural patterns described: all other invertebrates were undoubtedly rare, and the multivariate analyses were done on reduced datasets, excluding the rare species.

In the Westerschelde 17 species were common and only 8 species could be considered to be really abundant. This holds true for all salinity zones. Also in other European estuaries few species have been reported to dominate the epibenthic communities (*e.g* Nash & Gibson 1982, Henderson 1989, Elliott & Dewailly 1995). Still, two groups of stations always clustered together in the different multivariate analyses: stations 3-5 and stations 10-13. The higher salinity and oxygen saturation for the first group of stations was correlated with the presence of a variety of species, which mainly occurred in the polyhaline zone at low densities and biomasses. For example, shore crab *Carcinus maenas* is known to avoid low salinities during most of the year (De Veen *et al.* 1979). On the other hand a higher turbidity and - to a lesser extent - higher temperature characterized stations 10-13 with high densities and biomasses for only a few species.

Four main factors can explain the higher densities of shrimps, gobies and flatfish in the mesohaline zone: (1) in the subtidal area of the Westerschelde mysids are very abundant (Mees *et al.* 1993a). This offers a high food supply for fish species, which prey upon the hyperbenthos and zooplankton, such as gadoids and gobies (Chapter 7). In the Loire estuary, fish were mainly concentrated in areas with large trophic resources (Marchand 1993). (2) Large sandflats and sheltered mudflats are found in this part of the Westerschelde (Oenema *et al.* 1988). These intertidal areas harbour high macrobenthic biomasses (Ysebaert *et al.* 1993), which are preyed upon by epibenthic species such as flatfish during high tide (Chapter 7). (3) Mainly juvenile epibenthic life history stages (O- and I-group) are abundant in the Westerschelde. These can profit from the mesohaline conditions in turbidity, salinity and temperature, to escape from larger predators, which are probably less adapted to this environment (Potter *et al.* 1986). (4) The brackish tidal marshes, such as the marsh of Saeftinge, act as adjacent nursery areas for postlarval individuals of shrimps, gobies and flatfish (Cattrijsse *et al.* 1994).

The innermost brackish station (14) had a comparable epibenthic community as the group of stations 10-13. Probably, the high turbidity and muddy sediment in station 14 (K. Hostens, personal observation) provide favourable conditions for flatfish (mainly *Limanda limanda* and *Pleuronectes flesus*). The spatial separation for the other stations was not so clear, which also explains the low eigenvalues for both the first ordination axes. This could be due to the fact that the species in the 'other fish' group didn't show a clear preference for a specific salinity zone. The high number of species recorded at station 9 could be influenced through the connecting channel between the Oosterschelde and the Westerschelde. Indeed, some species mainly found at station 9, such as *Trigla lucerna*, *Zoarces viviparus* and *Engraulis encrasicolus*, were typical in the Oosterschelde during the eighties (Chapter 3-Add., Chapter 3).

Patterns in current velocity, current direction and waves, can affect the distribution, growth and survival of benthic species in shallow water communities (Barry & Dayton 1991). The most marine station off Vlissingen, characterized by a high transparency of the water, was separated in all analyses. The current velocities in the Westerschelde stay high up till Antwerp with an average of 70 cm s^{-1} (Claessens 1988), but probably the maximum current velocities at the mouth of the estuary were too high for the 'settling' of demersal species. Station 2 was located near a point where reflection of the tidal waves has to occur, while station 7 was located at the head of a sandflat which is mainly influenced by the flood tides (Vroon *et al.* 1997). Both stations 2 and 7 were characterized by sandeel, a typical species for exposed areas (Chapter 3). Station 6 was probably subject to the high tidal movement of the ebb tides, but in some analyses it was classified together with station 5. Both stations are characterized by somewhat higher average temperatures. The epibenthic community at these stations could deviate from that of other stations due to the water from the Canal Gent-Terneuzen that enters the Westerschelde between station 5 and 6.

2.4.2 Seasonality

In the Forth estuary 42 fish species were classified as marine (20), resident (12), fresh (4) and diadromous (5) (Pomfret *et al.* 1991). If the same classification were followed, the 37 fish species in the Westerschelde should be classified as 24 marine, 8 resident and 5 diadromous species. This kind of classification is based on the life history and abundance of the epibenthic species, and whether the marine species are juveniles or not (Elliott & Taylor 1989, Elliott & Dewailly 1995). The time of the year they appear in the estuary is not included in this classification. In the present study, the classification is based on the main season the epibenthic species are present in the estuary, and their main life stage and abundance during that period. As already noted, the abundant (A) and common (C) classes are mainly constituted of shrimps, gobies and flatfish, followed by clupeoids, crabs, gadoids, pipefish and sandeels (Table 2.2).

A fourth classification criterion, which takes into account the life history of the species, was not used. In this study 'resident' means that the species is present in the estuary during the whole year, but not necessarily during all life history stages. *Solea solea*, for example, were mainly found as juveniles (J) in the estuary during the whole year. Therefore they were classified as winter-resident (WR), which also specifies in what season they were most abundant. The invertebrate species *Crangon crangon* and *Carcinus maenas* were classified as summer-resident (SR). Most of the species classified as SR and WR, can also be placed in a group of 'estuarine' resident species. But these species also occur in marine coastal systems (Chapter 2-Add.2) and in other neighbouring systems like the marine embayment of the Oosterschelde (Chapter 3) or the brackish lake Grevelingen (Doornbos 1982). Perhaps a term 'brackish' species would be more appropriate. *Pomatoschistus microps* has been classified in most studies as an estuarine resident. During the early summer months this gobiid species was rarely found in the subtidal of the Westerschelde. It is known that in this period *P. microps* grows up in the adjacent salt marshes (Cattrijsse *et al.* 1994). The species then recruits to the subtidal of the estuary, which makes it an estuarine resident. But, based on the subtidal density data and on the modal length-class, *P. microps* has been classified as a winter elder (W,E) species. On the other hand, *Syngnathus rostellatus* (also classified as estuarine resident in other studies) was placed in the summer group (S) since it was nearly absent from the Westerschelde between December and April.

Most juvenile and some of the elder species in the Westerschelde can be classified as 'marine' species. In this study, it is specified in which period they have entered the estuary. *Trisopterus luscus*, for example, is a typical juvenile summer (J,S) species. During a short period of three months they grow from 50 to 130 mm in the estuary (modal length-class 70 mm). A typical juvenile winter (J,W) species is *Limanda limanda*: from September onwards only O+ individuals were found. In January two clear cohorts (0 and 1) could be detected. This is in accordance with observations in the estuaries on the west coast of Scotland as well as in the Wadden Sea (Elliott *et al.* 1990).

New in this study is the class of bimodal (B) species, mainly formed by the clupeid species. The individuals of both *Clupea harengus* and *Sprattus sprattus* in summer are small (modal length 50 mm), these of the winter cohort are larger (Table 2.2). The winter cohorts of both species are more abundant, but both abundance peaks for *C. harengus* are one month later. According to Elliott *et al.* (1990) the winter usage of estuaries by clupeoids is correlated with the higher turbidity, which protects these species from visual predators. Another bimodal species (normally classified as estuarine resident) is *Liparis liparis*, with small individuals (65 mm) occurring between May and July and larger ones (115 mm) in September to December. *L. liparis* was rare in January and absent from the estuary between February and April. This is in contrast with the findings of Potter *et al.* (1986) who noted a peak abundance in December-January in the Severn estuary.

Pleuronectes flesus is a catadromous species, but in contrast to other catadromous species elder individuals were recorded during the whole year, while from December to March also 1+ juveniles were found. It is therefore classified as a winter-resident (WR) species in this study. *Anguilla anguilla* on the other hand, was classified as elder summer (E,S) species, caught at the moment they pass through the estuary to spawn at sea. They were found in the mesohaline zone in May, while in September they were mainly caught in the polyhaline zone of the estuary.

Other studies state that estuarine environments are important nursery areas not only for juvenile marine fishes but also for anadromous species (Morin *et al.* 1992). In the Westerschelde, only two anadromous species (*Alosa fallax* and *Lampetra fluviatilis*) and one freshwater species (*Pungitius pungitius*) were recorded a few times. *Gasterosteus aculeatus* is a rather brackish species and was mainly found as winter elder (W,E) individuals. Van Damme *et al.* (1994) recorded six freshwater and one anadromous species in the lower Zeeschelde. Three of these were only caught once. In comparison with some fifty years ago, the total number of fish species in the Westerschelde estuary has been reduced from 67 to 37, although it is not always clear where exactly the species were recorded in the study by Poll (1945). Man-made structures such as sluices in the upper and middle reaches of the river Schelde, can form migration barriers. Still, the striking absence of freshwater and anadromous species is almost exclu-

sively correlated with the low oxygen concentrations upstream the Dutch-Belgian border. Most probably a regulated and slow sanation of the Schelde basin would be appropriate to enlarge and ensure the diversity of epibenthic communities. Large-scale and internationally coordinated reintroduction programmes will probably be necessary to bring back typical anadromous species such as sturgeon *Acipenser sturio*, sea lamprey *Petromyzon marinus* or salmon *Salmo salar*.

Although estuaries are used by many marine fish as nursery areas, only few species reproduce in the system (Wootton 1992). The clockwise arrangement of the monthly sample scores in the CCA illustrates the cyclical changes in abundance and species composition in the fish communities of the Westerschelde. In contrast with the findings of Potter *et al.* (1986), these seasonal changes can be largely explained by the four environmental variables that were measured. The plot of the species scores in the plane of the first two canonical axes was somewhat distorted by the high number of occasional species. Still, it mainly reflects the different periods of maximal densities, which can be brought back to the periods of immigration of the different species. Between July and October most summer juveniles and elder species from marine origin enter the estuary, and the resident species reach maximal densities through reproduction. September was plotted near most summer species in the CCA, but it is also the period when some of the overwintering species joined the summer community. Between October and December most of the occasional winter species reached a maximum density, while in January densities were highest for five of the ten abundant species. Potter *et al.* (1986) also found more estuarine dependent species between late summer and early winter. These data are in agreement with Elliott *et al.* (1990) who noted that marine juveniles and overwintering species are the most important epibenthic species in most estuaries.

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CHAPTER 2 - ADDENDUM 1 SPATIAL AND SEASONAL PATTERNS IN THE EPIBENTHOS OF THE WESTERSCHELDE

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2.1 Introduction

The upper part of the Westerschelde estuary, called the Westerschelde, extends from Vlissingen at the mouth towards Bath at the Dutch-Belgian border, in the southwestern part of the Netherlands. Monthly beamtrawl samples were taken in 1990 at 14 stations along a salinity gradient in the subtidal of the Westerschelde with R.V. 'Luctor' (34 m, 500 pk).

The epibenthos comprises the 0- and 1-group stages of the demersal fish species next to the larger mobile invertebrate species (mainly crustaceans). Forty-five epibenthic species were recorded, of which thirty-five species occurred with less than 1 individual per 1000 m². Different multivariate techniques were used to characterize the spatial and seasonal patterns in the epibenthos of the Westerschelde (also see §9.6.1).

Based on the current knowledge, some guidelines are given for future actions that should be undertaken to improve the epibenthic situation in the Westerschelde.

2.2 Spatial patterns

A Twinspan classification analysis, based on the yearly averaged biomass values, revealed four epibenthic communities in the Westerschelde, which are divided in a marine and a brackish part around Hansweert. A CCA ordination showed the same division in the plane of the first two axes, which is mainly correlated with 3 environmental variables. The marine communities are characterized by higher salinity and oxygen saturation, while the brackish part is correlated with a higher turbidity (calculated as the reciprocal value of the Secchi depth). The latter is also twice as rich (> 2000 ind./1000m²) in epibenthos as the marine part.

The composition of the communities for the important epibenthic categories is given in Fig. 2.8. Both communities are mainly dominated by shrimp

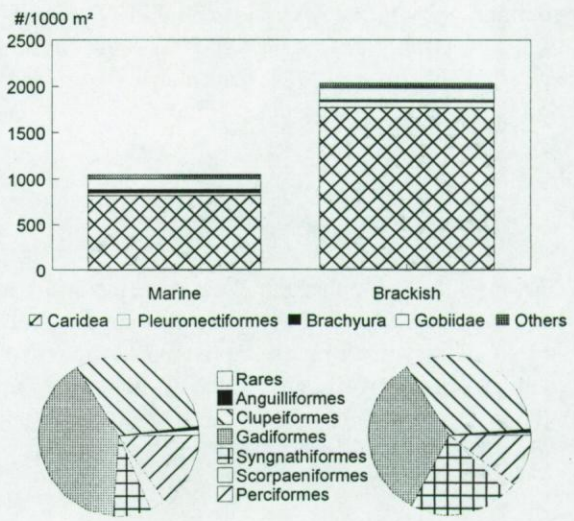

Fig. 2.8 Average density (ind $1000m^{-2}$) of the epibenthos in 1990 for the five main groups, and relative composition for the 'others' group, in the marine and brackish parts of the Westerschelde

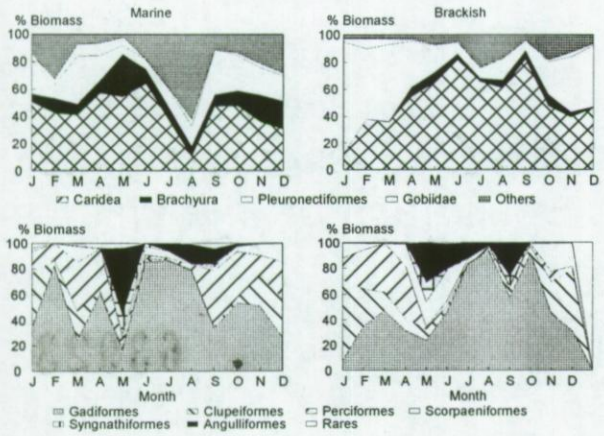

Fig. 2.9 Relative biomass (gADW $1000m^{-2}$) of the epibenthos in 1990 for the five main groups and for the 'others' group, in the marine and brackish parts

Crangon crangon, followed by gobies *Pomatoschistus minutus* and *P. lozanoi*, flatfishes *Limanda limanda* and *Pleuronectes platessa* and shore crab *Carcinus maenas*. The other important fish groups are gadoids and clupeoids.

2.3 Seasonality

Although not very clear, correspondence analysis revealed four major temporal segregations both in the marine and the brackish part. Still, a succession from month to month can be seen, with typical species in each community (Fig. 2.9).

The spring and summer months are characterized by juvenile epibenthic species, such as *P. lozanoi*, bib *Trisopterus luscus* and eel *Anguilla anguilla*. The autumn and winter months on the other hand are characterized by estuarine residents, such as common goby *P. microps* and sand goby *P. minutus*, or by overwintering species, such as sprat *Sprattus sprattus*, dab *Limanda limanda*, plaice *Pleuronectes platessa* and blenny *Zoarces viviparus*.

2.4 Human pressure

These results show that the Westerschelde still contains high numbers of some epibenthic species, but it is also characterized by an impoverished fauna. Due to high organic waste loads, the water quality upstream the Dutch-Belgian border is very bad. During most part of the year the oxygen concentrations drop below the threshold of 4 ppm, which makes it almost impossible for most marine animals to survive in that area. The number of fish species decreased with 40% in comparison with 1940. Mainly the diadromous fish species are rare or even absent from the Westerschelde.

Another important factor is the industrial pollution. It is not clear what is going to happen with the heavy metals, which are 'safely' bound to the sediment, with a sanation of the Schelde bassin. But due to high concentrations of PCB, starfish were not able to reproduce anymore, and thus have disappeared from the Westerschelde.

Also the continuous dredging in the main channel, next to sand exploitation on the sand flats and drainage of the flooding areas, resulted in a drastic change in the natural structure of the estuary, a 50% loss of marsh habitat and eroded mudflats. For the epibenthic communities in the Westerschelde, this means a reduction of their nursery and foraging habitat, which will put a damper on the importance of the Westerschelde for the North Sea fish stocks.

2.5 Conclusions

The Westerschelde can be divided into a marine and a richer brackish part. The communities still contain high numbers of some epibenthic species with a seasonal succession from marine juveniles to overwintering species.

But the epibenthos is also characterized by an impoverished fauna, due to human pressure. Based on the current knowledge, some future actions that should be undertaken to improve the epibenthic situation, are: slow sanation of the Schelde bassin, new dredging strategies, and of course forced limitation of the overfishing of the North Sea stocks.

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CHAPTER 2 - ADDENDUM 2 THE MOBILE EPIBENTHIC FAUNA OF SOFT BOTTOMS IN THE DUTCH DELTA (SOUTH-WEST NETHERLANDS): SPATIAL STRUCTURE

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Key words: North Sea; shallow coastal area; Westerschelde estuary; pollution; demersal fish: epibenthic crustaceans; starfish

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Abstract. *During 1989 monthly beam trawl samples were collected at 48 stations in the Dutch Delta. The annual mean densities of the demersal fishes and mobile epibenthic invertebrates at these stations were calculated. These data were then subjected to multivariate statistical techniques for an analysis of the spatial structure of the communities found and to study the relationship between these communities and their environment. The present study confirms the results of Henderson (1989) that, given a fairly limited number of environmental variables, mainly salinity and exposure/substratum type, quite accurate predictions of the type of community expected at a certain site can be made. The explicit inclusion of epibenthic invertebrates, a dominant group in most assemblages, in studies mainly targeted at demersal fishes, is strongly recommended. In the Dutch Delta rich and varied communities exist in the Voordelta. A number of groups, such as salmonids, anadromous species and starfish, expected in the Westerschelde are absent or extremely rare probably as a consequence of pollution stress. The Oosterschelde is relatively poor in density terms but has a highly diverse epibenthic fauna dominated by fishes.*

2.1 Introduction

Most studies reporting on fishes and larger epibenthic invertebrates (*e.g.* shrimps, crabs) are heavily biased towards the exploited life stages of commercial species. Despite general agreement on the qualitative notion that estuaries and shallow coastal areas are important nurseries for marine fishes (Haedrich 1983) there is still a need for quantitative studies. In comparison to macrobenthic studies there are relatively few studies describing the structure of estuarine fish communities and these have been mainly restricted to British estuaries (Claridge *et al.* 1986, Henderson 1989, Elliott *et al.* 1990). Some comparative exercises have been done (Costa & Elliott 1991, Pomfret *et al.* 1991) and functional studies are beginning to emerge (Elliott & Taylor 1989, Chapter 3). Process studies have as yet been restricted to single species of commercial importance (*e.g.* van der Veer 1986).

The development of multivariate statistical techniques has created the possibility of summarising the structure in large multispecies data sets. These techniques are very popular in many ecological fields (review in James & McCulloch 1990) but have rarely been used in studies of marine fishes of the North Sea. Henderson (1989) used Principle Component Analysis to analyse the structure of the fish communities as recorded from the intake screens of power stations in England and Wales. Daan *et al.* (1990) applied an unspecified type of cluster analysis to the fifty most abundant fish species recorded in the Eng-

lish Groundfish Surveys 1982-1985. Though the sampling gears deployed to sample fish catch a number of mobile epibenthic invertebrates, these animals are rarely integrated into the results.

In this study a multivariate analysis of the spatial structure of the mobile epifauna of the Dutch Delta, on the basis of annual mean density and biomass, is presented. The study is restricted to soft bottoms. An attempt is made to assess the correlation between the occurrence of a certain species assemblage and its environment. A lot of detail is provided on the practical strategy for the multivariate analysis. These details are not often reported in papers but may be important to judge if the choice of the technique and the way in which it was applied were adequate (James & McCulloch 1990).

The purpose of this study is to provide a baseline for future functional and process studies of the mobile epifauna of the Delta area and of the Westerschelde in particular. These will have to be based on spatial units coinciding with the biological communities. To comply with international standards a massive reduction of the pollution load of the Westerschelde will have to be achieved in the (near?) future and the impact assessment of these changes will hopefully be monitored. A baseline study is a prerequisite for such a monitoring programme.

2.2 Materials and methods

2.2.1 Study area (Fig. 2.10)

The Rhine, Meuse and Schelde, the three main European rivers, enter the North Sea in the Dutch Delta region in the south-western part of The Netherlands. Most of the former estuaries in this area have been altered by man (review in Heip 1989b). The study area covers only three parts of the Dutch Delta: the Westerschelde, the Oosterschelde and the central part of the Voordelta.

The lower part of the river Schelde is generally known as the Westerschelde estuary. It is the last remaining true estuary in the Dutch Delta and exhibits marked gradients in salinity, oxygen and turbidity. The mean fresh water load is 105 $m^3.s^{-1}$ (Herman *et al.* 1991). The input of organic and inorganic pollutants is very high, especially in the brackish part (Duursma *et al.* 1988, Van Eck *et al.* 1991). The division between the marine and the brackish part is situated between stations W8 and W9 (Fig. 2.10) (Hummel *et al.* 1988b).

The former Oosterschelde estuary is now a tidal inlet of the Southern Bight of the North Sea. By the construction of a number of dams in the landward part, the fresh water inflow was reduced to 55 $m^3.s^{-1}$ and in 1986 a storm-surge barrier was completed at the mouth. This caused substantial changes in the functional characteristics of the ecosystem (Bakker *et al.* 1990). Some impact could also be detected on the fishes and epibenthic invertebrates (Chapter 3-Add., Chapter 3).

The Voordelta is the shallow coastal area formed by the interlinked ebb-tidal deltas of the (former) estuaries of the Dutch Delta. It extends from the Belgian-Dutch border in the South to the Hoek van Holland in the North. Its marine boundary is arbitrarily defined by the Mean Tidal Level (MTL) -10 m isobath. The closure of the former estuaries has had an important impact on the geomorphology (Louters *et al.* 1991) and ecology (Chapter 4-Add.) of the area. Only the central part of the Voordelta, the ebb-tidal delta of the former Grevelingen estuary and the ebb-tidal delta of the Oosterschelde, have been investigated in this study.

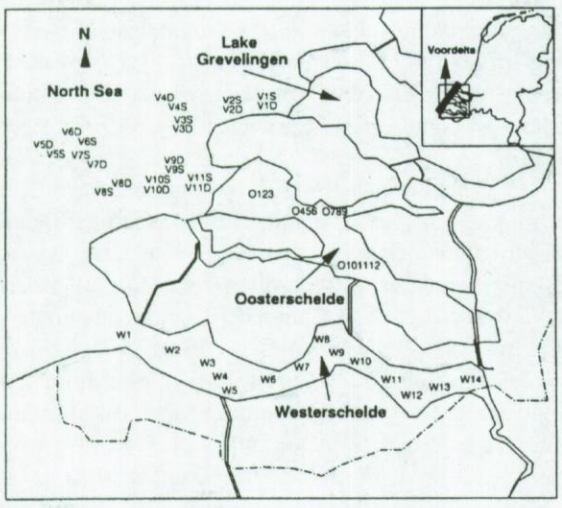

Fig. 2.10 Map of the study area with the sampling stations

2.2.2 Sampling

During 1989 monthly samples were taken at 22 stations in the Voordelta, 12 stations in the Oosterschelde, and 14 stations in the Westerschelde (Fig. 2.10). In the Voordelta the 22 stations cover two depth strata (MTL –5 m and MTL –10 m) at eleven localities. In the Oosterschelde the 12 stations correspond to three parallel tows at four localities. In the Westerschelde the stations are located at the edges of the ebb-tidal channel from the mouth to the Dutch-Belgian border. Several trials were made to sample further upstream but, due to the inordinate amount of rubbish covering these grounds, gear loss was so frequent that no results can be reported (see also Pomfret *et al.* 1991).

In January and August the six most seaward stations of the Voordelta could not be sampled because of adverse weather conditions. Five other Voordelta samples and 5 Westerschelde samples were lost because the net was torn or the beam trawl hit an obstacle.

Samples were taken from the R.V. Luctor (34 m, 500 Hp) using a 3-m beam trawl, equipped with a 6-m long net with a 5 x 5 mm mesh in the cod end, a tickler chain and a chain in the groundrope. Hauls were 1 km in length. Ship speed relative to the bottom when trawling was on average 4.5 knots. All fishes, with the exception of the gobies, were identified to species level on board. Gobies of the genus *Pomatoschistus* were preserved for identification in the laboratory (Hamerlynck 1990). As the invertebrates were treated more or less in bulk, a number of rare species were overlooked: the shrimps *Crangon allmani*, *Pontophilus trispinosus*, *Processa modica modica* and *Pandalus montagui*, the crabs *Portumnus latipes*, *Liocarcinus arcuatus* and *Macropodia rostrata*. Specimens of these species were occasionally observed in the Voordelta but were not quantified. *C. allmani*, *P. montagui* and the three crab species mentioned were sometimes also noted in the Oosterschelde catches. In the Westerschelde *Palaemonetes varians* was seen occasionally. Although the hermit crab *Pagurus bernhardus* occurs commonly, this crab was not quantified. Sometimes Cephalopoda and Echinodermata Crinoidea were caught but not quantified.

Standard length was recorded for all fish specimens. Biomass was calculated from length - Ashfree Dry Weight (ADW) regressions compiled for the Dutch Delta (see Tables 4.2 and 5.2). Invertebrates were counted and (wet)weighed. Net efficiency was assumed to be 20 % for all size classes of fish and invertebrates. This assumption is based on the work of Kuipers (1975) on plaice. For the relatively immobile starfish efficiency was assumed to be 40 %. Efficiency adjusted densities are given as N per 1000 m², biomass as gADW per 1000 m².

2.2.3 Environmental variables

At each site salinity (ppt), water temperature (°C), water depth (m), Secchi disk depth (m) and oxygen content (mg l^{-1}) were measured. Salinity, temperature and oxygen content were measured at about 1 m above the bottom. For these variables means were calculated per station. These averages are not true annual means because they were only calculated for those months in which all stations were sampled. The measurements in January and August were therefore not included in the calculations. In November no measurements could be taken because of a technical failure of the probe.

In December 1988 hyperbenthos samples were taken with a hyperbenthic sledge at all the stations according to the methodology described in Mees & Hamerlynck (1992). The hyperbenthic biomass data (mgADW m^{-2}) were taken from that study. At each sampling station of the Westerschelde and Oosterschelde three Van Veen grabs were taken and sieved over a 1-mm mesh. Macrobenthic biomass (gADW m^{-2}), mud content (%) and median grain size of the sand fraction (mm) were measured. Macrobenthic biomass data for the Voordelta stations were taken from Craeymeersch *et al.* (1990). The sediment composition data for the Voordelta and the 1% wave height (the wave height exceeded for 1 % of the year) were taken from van Dijke & Buijs (1987). Benthic biomass data were collected to investigate possible correlations between epifauna and their main food. Wave height is used as a measure of exposure.

Table 2.3 Ranges of the environmental variables measured, with (between brackets) the station at which the extremes were recorded, the mean for all stations and the standard deviation of that mean

VARIABLE (unit)	MINIMUM	MAXIMUM	MEAN	S.D.
Salinity (ppt)	13.4 (W14)	32.1 (V7)	28.5	5.0
Temperature (°C)	11.5 (V2)	13.2 (W14)	12.0	0.4
Depth (m)	5.3 (V1S)	21.7 (OR2)	10.4	3.7
Secchi depth (m)	0.5 (W14)	3.3 (OW)	1.9	0.9
Oxygen (mg.l^{-1})	7.4 (W14)	10.6 (V2)	10.0	0.5
Hyperbenthos (mg ADW.m^{-2})	0.02 (OW)	242 (W14)	19.4	56
Macrobenthos (g ADW.m^{-2})	0 (W12-W14)	90 (V1D)	7.2	18
Mud content (%)	0 (V4D,W6,W11)	20 (V1D)	2.8	3.7
Median grain size (µm)	125 (V1D)	357 (W3)	230	56
1% significant wave (m)	1 (OW,W11-W14)	3.5 (V5)	1.8	0.7

Table 2.3 summarises the range of the environmental variables recorded. It should be noted that only the means per station are shown and that in some months more extreme values have been recorded, *e.g.* 4 mg l^{-1} of oxygen in April at station W14.

2.2.4 Multivariate analysis of community structure

Density and biomass data from each haul were subjected to a fourth root transformation prior to further analysis (Clarke & Green 1988). This transformation partly compensates for the deviation from normality typical for species abundance data. The transformed data set then still contains an inordinate amount of zero observations. Eliminating rare species (Field *et al.* 1982, Henderson 1989, Daan *et al.* 1990) may alleviate this, but it entails a loss of information. In the present, relatively species-poor data set, no *a priori* reduction of the number of species was accomplished.

All hauls at a sampling station were considered to be replicates and the annual means of (the transformed) density and biomass were calculated.

The data were subjected to a Two Way Indicator Species Analysis (TWINSPAN) (Hill 1979) and a Group Average Sorting (GAS) using the Bray Curtis similarities (Bray & Curtis 1957). The clusters of stations distinguished by both techniques were then compared. The choice of the cut levels in the TWINSPAN was based on the simple rule of thumb that the number of observations (*e.g.* density values) within each cut level should be approximately equal, except for the lowest cut level which contains all the zero observations and the two highest cut levels which contain approximately half as many observations as the other levels. In this way some extra weight was given to the most common species. Cut levels chosen for the density data were 0, 0.11, 0.2, 0.4, 0.7, 1.2, 2.1 and 3. For the biomass data these were 0, 0.15, 0.36, 0.81, 1.59, 2.3 and 4.2. All other settings in the TWINSPAN are default, with the exception of the maximum number of divisions, which was set to four instead of six.

The data were then subjected to ordination techniques from the CANOCO package (Ter Braak 1987). A Correspondence Analysis (CA) was done to assess total community variability and to compare the scales of the species scores and the sample scores (Ter Braak & Prentice 1988, Jongman *et al.* 1987). Next, a Principal Component Analysis (PCA) was performed, combining the biotic data with the environmental variables.

In the PCA euclidean distances were calculated from the correlation matrix (James & McCulloch 1990). Environmental variables were centred, i.e. replaced by the deviation from the mean for all stations (Jongman *et al.* 1987). As the underlying response model of PCA is linear, the hyperbolic relationship which was found between Secchi disk depth and the first ordination axis was linearised by a reciprocal transformation of this variable.

When characterizing a community, Hill's diversity numbers (Hill 1973) of the order 0, 1, 2 and $+\infty$ are of particular interest (Heip *et al.* 1988). For each of these Hill numbers the means and standard deviations were calculated per assemblage. With increasing order of the Hill number, the influence of dominant species increases and the influence of species richness decreases (see also Mees *et al.* 1993b).

2.2.5 Terminology

All Voordelta samples were taken in inshore waters but to simplify the description of the results the most seaward stations (V5 to V7) are labelled 'offshore' stations in comparison to the stations V1 to V3 and V9 to V11 which are labelled 'inshore'. The V4 and V8 stations are labelled 'intermediate'. The word 'locality' refers to a broader site including two stations in the Voordelta (*e.g.* locality V1 is composed of stations V1S and V1D) and three stations in the Oosterschelde. In the figures species names were shortened to the first four letters of the genus and the first four of the species name.

2.3 Results

2.3.1 Species composition

Fiftythree species were quantified (Table 2.4). These species are classified into six ecological types according to the use they make of estuarine areas (Elliott & Taylor 1989, Costa & Elliott 1991). Eighteen species are truly marine and do not depend on estuaries for any part of their life-cycle (MO in Table 2.4), sixteen species are estuarine resident species (ER), ten marine species make use of the estuary as a nursery ground (MJ), five species are catadromous or anadromous (CA), three marine species spend part of the year in the estuarine environment as adults (MS). The three-spined stickleback *Gasterosteus aculeatus* is difficult to classify. It is partly a freshwater species, partly an estuarine resident (FW/ER).

2.3.2 Spatial structure

The results of the analyses with the biomass data were very similar to those of the corresponding analyses using the density data. Therefore, except for the TWINSPAN, only the density results are reported.

2.3.3 Classification

The result of the TWINSPAN (first division, eigenvalue 0.13) using the density data is shown in Fig. 2.11 (top). The first division separates the Westerschelde stations from the rest. Within this last group the next division separates a cluster mainly composed of offshore and intermediate Voordelta stations (VX). In the Westerschelde cluster the next division splits the stations in the brackish part (WB) from the stations in the marine part (WM).

Further divisions in the central cluster first separate the Oosterschelde stations from the inshore Voordelta and then split each of these into two smaller groupings. Thus four clusters are created:

- the deep inshore stations in the ebb-tidal delta of the Oosterschelde (VIO)
- the inshore stations in the ebb-tidal delta of the Grevelingen (VIG)
- the stations in the most landward part of the Oosterschelde (OI)
- the more seaward stations of the Oosterschelde (OO)

Table 2.4 List of the species quantified with their abundance (N per 1000 m²) in the different assemblages and their ecological type (for abbreviations see text)

	Assemblage							
	VX	VIO	VIG	OI	OO	WM	WB	
Species name								
Lampetra fluviatilis						<0.1		CA
Anguilla anguilla	<0.1	0.5	0.1	0.1	0.9	0.3	0.6	CA
Clupea harengus	11	20	62	3	10	3	6	MJ
Sprattus sprattus	22	7	29	18	3	24	18	MJ
Alosa fallax							0.1	CA
Engraulis encrasicolus	<0.1		<0.1	<0.1	0.1	0.1	0.1	ER
Gadus morhua	0.2	1	1		0.2	0.2	0.2	MJ
Merlangius merlangus	3	23	54	2	7	3	<0.1	MJ
Trisopterus luscus	0.8	7	10	7	11	1	2	MJ
Trisopterus minutus				<0.1	0.1			MO
Ciliata mustela	<0.1	0.4	2	0.1	0.1	0.2	0.6	MS
Zoarces viviparus	<0.1		0.3	3	0.6		0.2	ER
Atherina presbyter	0.1	0.7	0.6	1	0.1	<0.1	<0.1	ER
Gasterosteus aculeatus	0.2				0.3		0.3	FW/ER
Syngnathus acus	0.1		0.1	0.4	0.1		<0.1	ER
Syngnathus rostellatus	4	6	12	15	3	4	7	ER
Entelurus aequoreus	<0.1		<0.1	0.1	<0.1			MO
Trigla lucerna	0.3	0.4	0.8	0.4	0.1	0.1	<0.1	MJ
Myoxocephalus scorpius	0.1	1	0.5	1	0.2	0.1	0.3	ER
Taurulus bubalis				0.1	<0.1			MO
Agonus cataphractus	0.2	4	9	0.8	0.1	0.3	0.4	ER
Liparis liparis	0.1	2	1		<0.1	0.7	0.6	ER
Dicentrarchus labrax		0.1		<0.1			0.1	MJ
Trachurus trachurus	<0.1			3		0.4	<0.1	MO
Mullus surmuletus	0.3	0.6	0.3	<0.1				MO
Mugilidae species			0.5	0.1	0.2	0.1	0.1	CA
Trachinus vipera	0.2							MO
Pholis gunnellus			0.6	0.4	<0.1			ER
Ammodytes tobianus	26	0.7	2	0.1	0.5	4	2	ER
Hyperoplus lanceolatus	2		0.1			0.7	<0.1	MO
Callionymus lyra	10	42	25	15	0.7			MO
Pomatoschistus microps	<0.1			0.7	0.3	3	3	ER
Pomatoschistus pictus	4	4	5	0.3	0.2	<0.1		MO
Pomatoschistus minutus	50	64	506	161	37	39	118	MS
Pomatoschistus lozanoi	105	38	221	3	2	143	192	MS
Aphia minuta	0.2	1	2		0.1			MO
Gobius niger				<0.1				ER
Scophthalmus rhombus	0.1		0.1	0.2	0.2	<0.1		MO
Scophthalmus maximus	0.1		0.1					MO
Pleuronectes platessa	3	48	19	63	25	3	13	MJ
Limanda limanda	14	67	133	43	8	11	44	MJ
Pleuronectes flesus	0.1	1	2	0.2	<0.1	0.4	5	CA
Solea solea	0.2	12	9	2	0.7	4	8	MJ
Buglossidium luteum		0.1	0.2					MO
Microstomus kitt				0.3				MO
Arnoglossus laterna	<0.1							MO
Crangon crangon	697	1224	3071	446	460	1358	2467	ER
Liocarcinus holsatus	44	122	572	16	10	9	2	MO
Carcinus maenas	1	15	42	73	7	21	12	ER
Cancer pagurus	0.1	0.9			0.1			MO
Eriocheir sinensis							<0.1	ER
Homarus gammarus				<0.1				MO
Asterias rubens	175	1226	5426	106	132			ER

The TWINSPAN result (first division eigenvalue 0.14) for the biomass data (Fig. 2.11, bottom) resembles the result for the density data, though the order in which the groupings are separated and the indicator species may differ. Some stations are in a different cluster when comparing both results. Station W1, in the mouth of the Westerschelde is found in the WB cluster of the biomass result. Station V3D from the ebb-tidal delta of the Grevelingen is classified into the VIO cluster in the density result.

In the GAS the same four major clusters WS, OS, VI (this time without V10D) and VX, can be recognized as separate entities (Fig. 2.12). Within the

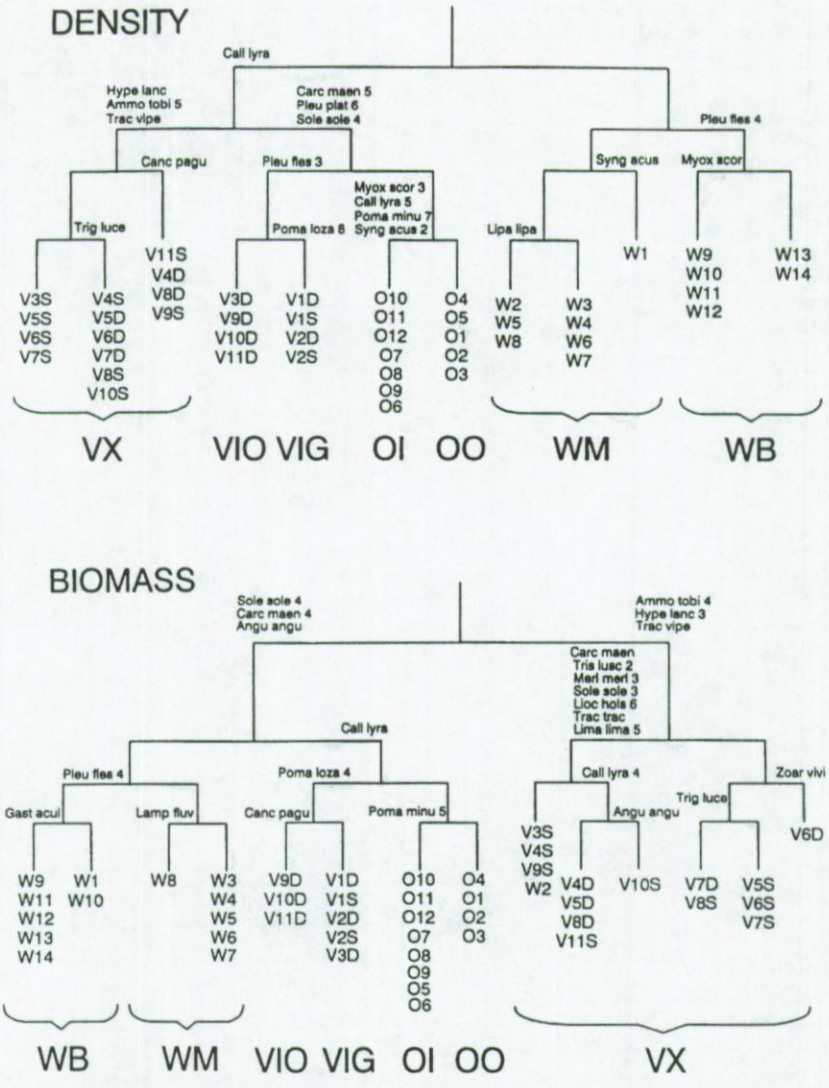

Fig. 2.11 Results of the TWINSPAN for density (top) and biomass (bottom). Indicator species are indicated with their cut level (level 1 is not indicated)

WS cluster the WB cluster lacks the stations W9 and W12. In the VX cluster (which now includes V10D) there is a subcluster grouping the shallow offshore stations and V8S. In the OS cluster the three stations from each of the four localities form tight clusters. In the VI cluster the VIG stations are found in close association. Station V3D is again closely associated to the VIO stations V9D and V11D.

2.3.4 Characterization of the species assemblages

From the results of the classification techniques it is clear that seven different clusters of stations can be defined comprising two in the Westerschelde (WM and WB), two in the Oosterschelde (OW and OE) and three in the Voordelta (VX, VIG and VIO). Station W1 was included in the WM cluster on the basis of the TWINSPAN using the density data and the GAS results. Station V3D was included in the VIG cluster on the basis of the TWINSPAN using the biomass data.

The densities of the various species in the assemblages corresponding to the different clusters are given in detail in Table 2.4 and are summarized in Fig. 2.13. Only fourteen species account for more than 1 % of the density in any of the communities thus defined. These species are starfish (*Asterias rubens*), brown shrimp (*Crangon Crangon*), swimming crab (*Liocarcinus holsatus*) shore crab (*Carcinus maenas*), sand goby (*Pomatoschistus minutus*), lozano's goby (*Pomatoschistus lozanoi*), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), sprat (*Sprattus Sprattus*), herring (*Clupea harengus*), sandeel (*Ammodytes tobianus*), dragonet (*Callionymus lyra*) and bib (*Trisopterus luscus*).

The VX assemblage has the lowest total abundance among the Voordelta clusters (Fig. 2.13). It has few starfish and very few flatfish. It has the highest densities of its indicator species *A. tobianus* and greater sandeel (*Hyperoplus lanceolatus*) and is

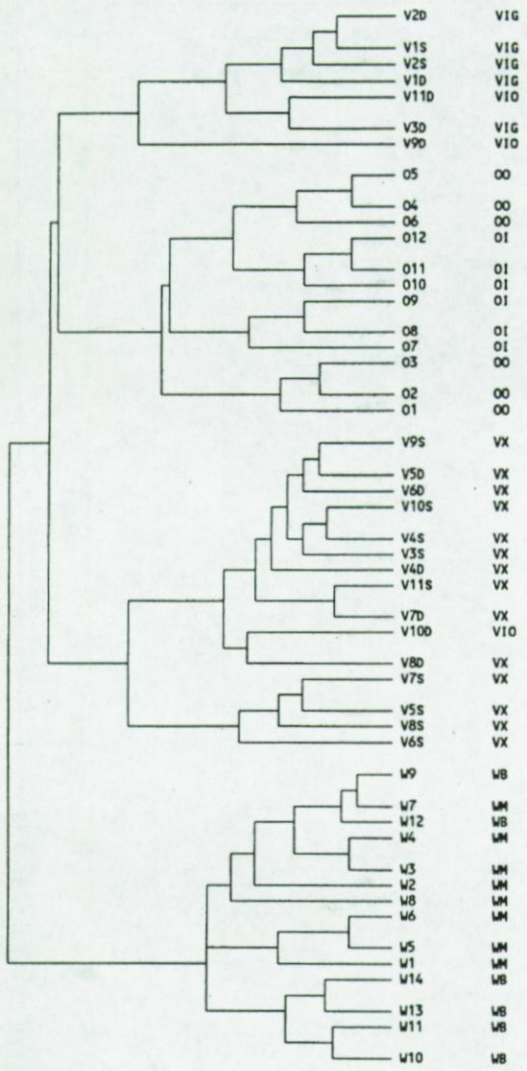

Fig. 2.12 Results of the Group Average Sorting using the Bray-Curtis similarities. Station names are followed by their classification into assemblages on the basis of the TWINSPAN results

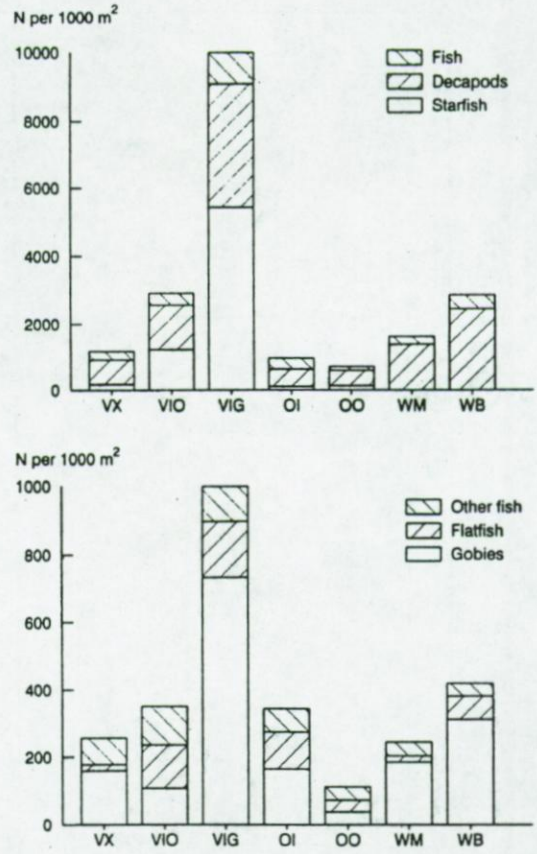

Fig. 2.13 Total density and composition of the different species assemblages for the three main taxonomic groups (top) and the three main fish groups (bottom)

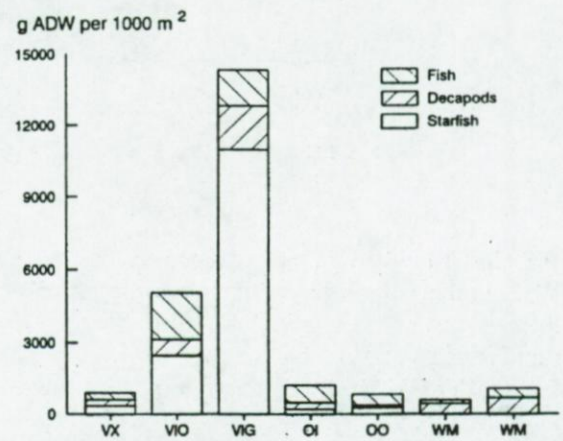

Fig. 2.14 Total biomass and composition of the different species assemblages for the three main taxonomic groups

the only group of stations in which the lesser weever *Trachinus vipera* and the scaldfish *Arnoglossus laterna* were recorded (Table 2.4).

The VIO assemblage has an intermediate total abundance. It is poorer than the VIG assemblage for almost all species except for *C. lyra*, *P. platessa*, sole (*Solea solea*) and its indicator species edible crab (*Cancer pagurus*).

The VIG assemblage has the highest total abundance being more than three times higher than in any other assemblage. *C. harengus*, *S. Sprattus*, whiting (*Merlangius merlangus*), *P. minutus*, *P. lozanoi*, *L. limanda*, *C. Crangon*, *L. holsatus* and *A. rubens* plus a host of less abundant species all reach their peak densities in this assemblage.

The OI assemblage has a low total abundance. It has, however, the highest *P. platessa* densities and also the peak densities of a number of species that are rare in the study area as a whole. The latter species are eelpout (*Zoarces viviparus*), sands melt (*Atherina presbyter*), scad (*Trachurus trachurus*) and three pipefish species (*Syngnathus acus*, *S. rostellatus* and *Entelurus aequoreus*). It is also the only assemblage in which the black goby (*Gobius niger*), the lemon sole (*Microstomus kitt*) and the lobster (*Homarus gammarus*) were recorded.

The OO assemblage has the lowest total abundance. Only the poor cod (*Trisopterus minutus*) has its peak abundance in this assemblage. Both Oosterschelde communities have exceptionally low abundances of *P. lozanoi*. The Oosterschelde is the

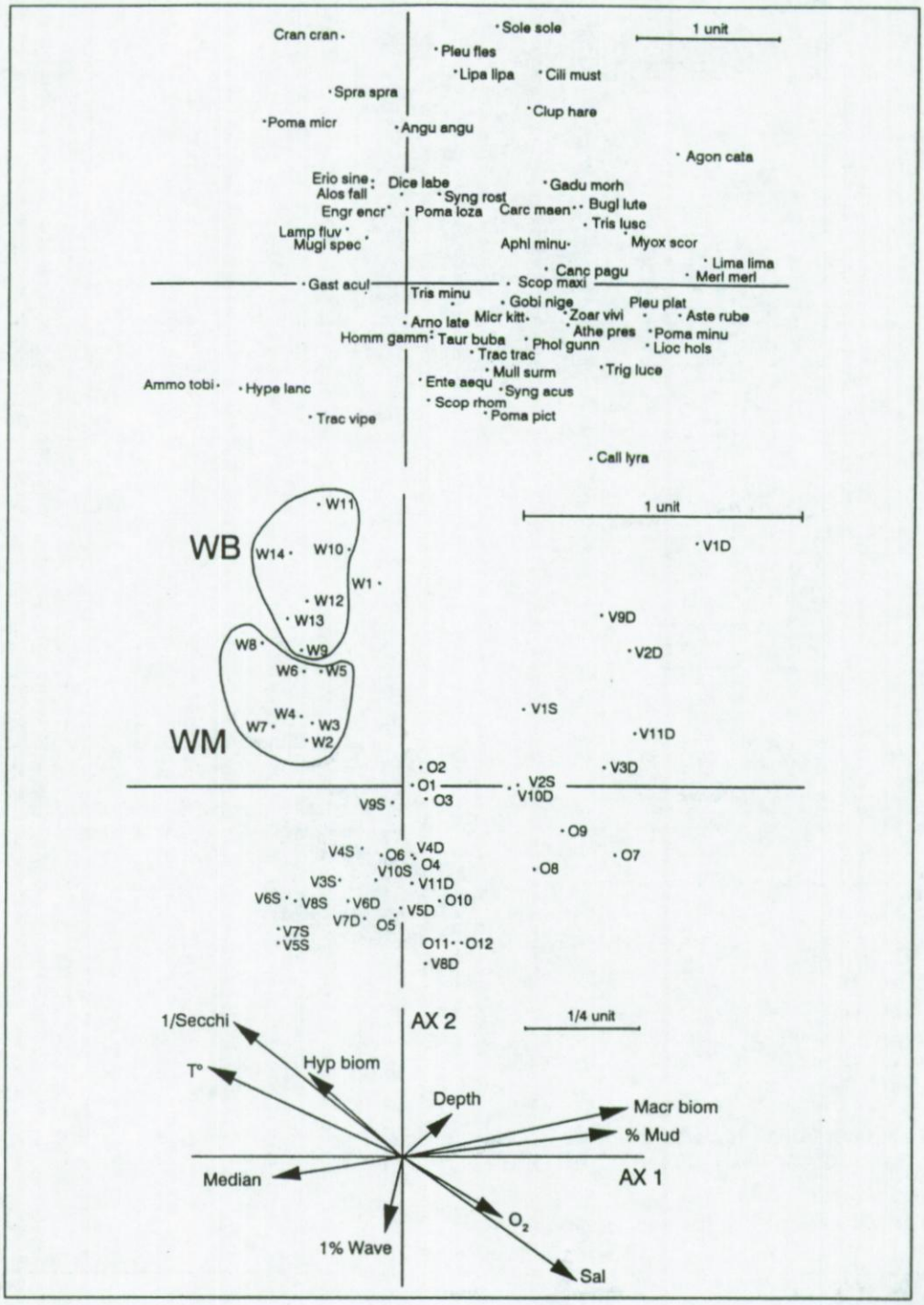

Fig. 2.15 Result of the Principal Component Analysis for the first two axes. The species scores (top), the sample scores (centre) and the environmental biplot (bottom) have different scales

only area were *T. minutus* and the sea scorpion (*Taurulus bubalis*), a rocky shore species, were recorded.

The WM assemblage has an intermediate abundance. Except for the only record of lampern (*Lampetra fluviatilis*) there are no typical species.

The WB assemblage has a somewhat higher total abundance than the WM assemblage. It has the highest densities of its indicator species flounder (*Pleuronectes flesus*). Notable but rare species are twaite shad (*Alosa fallax*) and mitten crab (*Eriocheir sinensis*), both only recorded in this assemblage. The absence of starfish in the Westerschelde is a distinguishing feature. The common goby (*Pomatoschistus microps*) reaches its highest densities in the Westerschelde.

Biomass composition for the three main groups fish, decapods and starfish is shown in Fig. 2.14. It can be seen that the dominance of the invertebrate groups in the Voordelta clusters is even

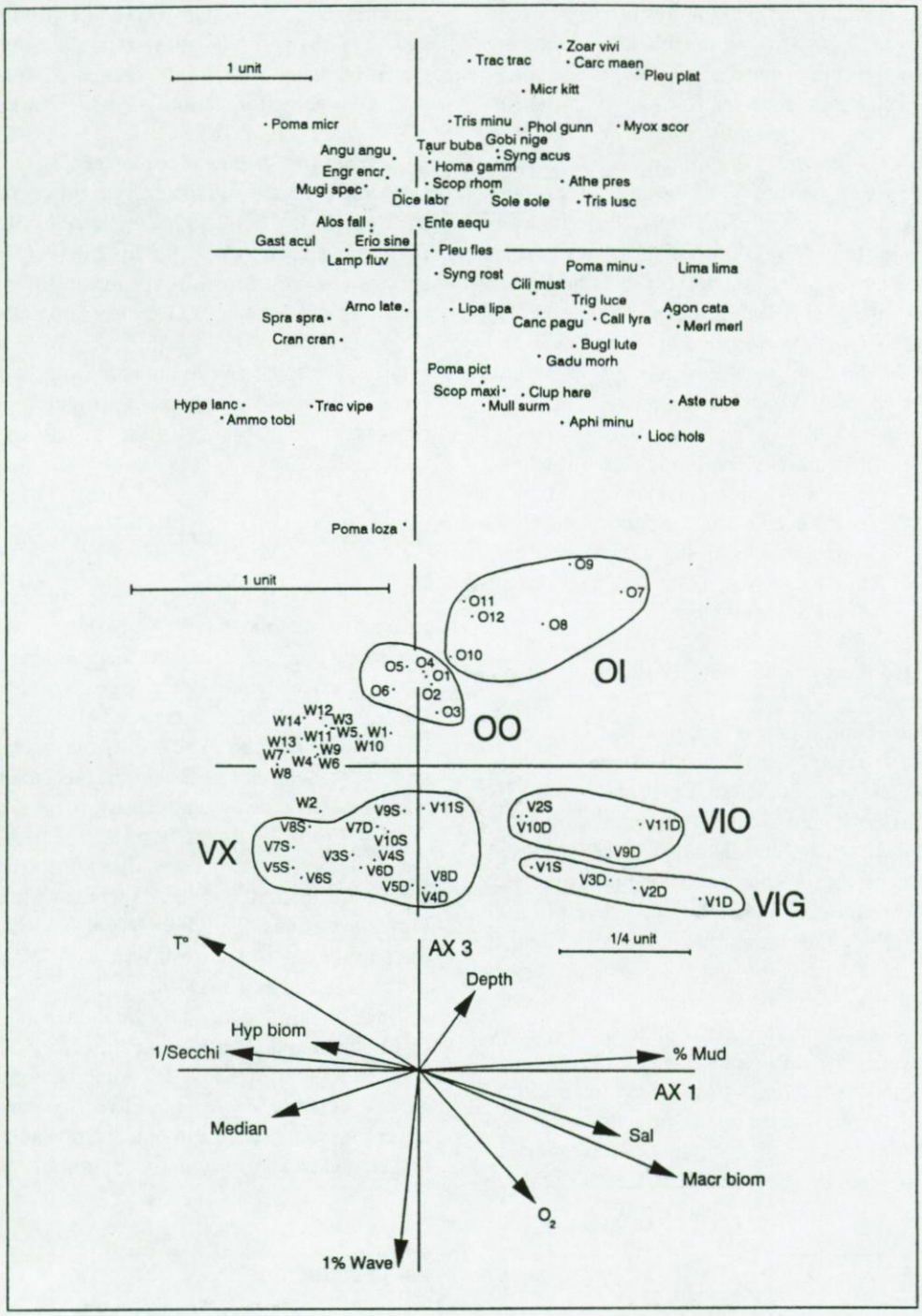

Fig. 2.16 Result of the Principal Component Analysis for the first and third axes. The species scores (top), the sample scores (centre) and the environmental biplot (bottom) have different scales

stronger than in density terms. Fish are the dominant group only in the Oosterschelde.

2.3.5 Relation to the environmental variables

The total community variability, which corresponds to the distance between the two most extreme stations along the first axis, as measured in units of scale (1 unit scale equals 1 unit standard deviation by definition) in the CA (not depicted) is only 1.2 units. This result means that a linear response model is most appropriate for the data. Moreover, most species have their optima outside of the range covered by the sampling because the scale of the species scores in the CA is 7.3 times smaller than the scale of the sample scores. Therefore, we choose PCA for the ordination with the environmental variables (Ter Braak & Prentice 1988, Jongman *et al.* 1987).

The first PCA axis has an eigenvalue of 0.16, both the second and third axes have eigenvalues of 0.13. In the plain formed by the first and the second PCA axis the sample scores clearly separate the

totality of Westerschelde stations from the rest of the Delta area (Fig. 2.15). All Westerschelde stations are located in the left upper quadrant which, in the corresponding species plot, contains *C. Crangon*, *S. Sprattus*, *P. microps*, eel (*Anguilla anguilla*), sea bass (*Dicentrarchus labrax*), *A. fallax*, *L. fluviatilis*, Mugilidae species, anchovy (*Engraulis encrasicolus*), *Eriocheir sinensis* and *G. aculeatus*. Interestingly, these species do not necessarily have their highest abundances in these stations but they are a constant and prominent feature of the Westerschelde stations. The stations corresponding to the WB and WM assemblages are separated along the second axis, except for W1 which associates with the WB cluster.

The other stations are plotted as a diagonal string with, at the left lower extreme, the shallow stations at the marine edge of the Voordelta (V3S through V8S), corresponding to the indicator species of the VX assemblage in the lower left quadrant of the species plot. This assemblage, characterized by *A. tobianus*, *H. lanceolatus* and *T vipera*, has a clear preference for the dynamic sands at the edge of the ebb-tidal delta.

In the central part of the plot there is a mixture of Voordelta and Oosterschelde stations. In the right upper quadrant one finds the stations of the VIG and VIO clusters. From the environmental biplot it is clear that the first axis correlates strongly with mud content and its covariable macrobenthic biomass. These two variables are negatively correlated to median grain size. The second axis correlates most strongly with the estuarine gradient in the Westerschelde with low water transparency (high 1/Secchi disk depth), high temperature and high hyperbenthic biomass towards the left upper corner and high oxygen content and high salinity towards the lower right.

In the plain formed by the first and third axes of the PCA the stations divide into an Oosterschelde cluster which can be separated into the OO and OI clusters, the VI cluster where the VIO (now with station V2S) and VIG clusters can be distinguished, the VX cluster and a tight cluster of Westerschelde stations (except for station W2 which lies close to the VX cluster) (Fig. 2.16).

In the species plot the species typical for the Oosterschelde are found in the right upper quadrant. In the right lower quadrant the species closest to the first axis are characteristic for the VIO cluster, the species towards the extreme lower right corner are those typical for the VIG cluster, notably *A. rubens* and *L. holsatus*.

From the environmental biplot it is clear that the third axis shows a strong correlation with the 1% significant wave, which itself is negatively correlated with depth.

2.3.6 Diversity (Fig. 2.17)

The average number of species recorded per station in each assemblage (N_0) is highest in the inshore Voordelta and Oosterschelde assemblages and lowest in the Westerschelde assemblages. Note that, though the highest number of species (41) was recorded in the VX assemblage (Table 2.4) the average number per station (N_0) is lower than in the other Voordelta and Oosterschelde assemblages.

From the diversity measures of higher order the exceptional character of the OI cluster is apparent. In this assemblage forty species were recorded at only six stations. The high N_1, N_2 and N_∞ measures are mainly due to the locality in the Northern branch of the Oosterschelde (O7,8,9 in Fig. 2.10). The three stations at this locality are dominated by *A. rubens*, *C. Crangon* and *P. minutus* and have low densities of a host of other species. The other communities exhibit a steadily decreasing diversity for all higher order measures when moving from seaward to landlocked and finally to estuarine conditions.

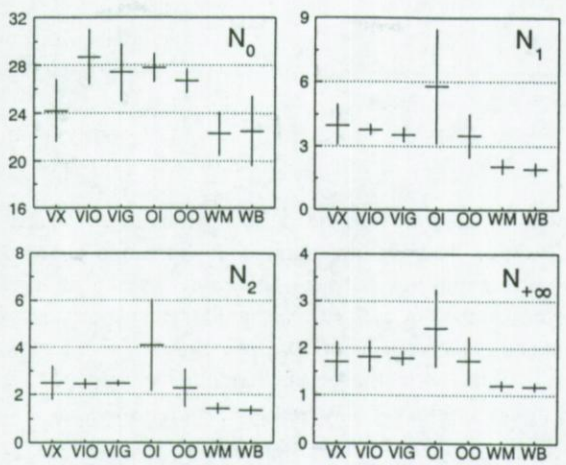

Fig. 2.17 Means of the Hill diversity numbers N_0, N_1, N_2 and $N_{+\infty}$ for the different species assemblages with their standard deviations

2.4 Discussion

The typical beam trawl surveys designed for monitoring of fishes are also very efficient for catching mobile epibenthic invertebrates. These invertebrates are a dominant component in each assemblage and the information inherent in the occurrence of these animals should therefore be used. The present study also suffers partially from this interference, at least for some of the less abundant species. Though each fish was examined in detail, the invertebrates were treated in bulk and only occasionally, *e.g.* in small catches, the rarer invertebrates were noticed. It seems likely for instance that *Pontophilus trispinosus* and *Portumnus latipes*, though rare, are typical members of the VX community. The exceptionally high diversity of the Oosterschelde, especially as measured by N_1

would also be even more spectacular if all invertebrates found had been quantified. Community structure is, at least partly, determined by species interactions such as competition and predation. These interactions are not limited to either fish-fish or crab-crab but go across taxonomic boundaries. Some of these predatory interactions are structurally important, *e.g.* shrimp-plaice (van der Veer 1986), whiting-shrimp (Henderson & Holmes 1989). Evidence on competitive interactions is less conclusive, but many species are known to share the same food (Costa & Elliott 1991, Le Mao 1986). Therefore, it is recommended that future studies reporting primarily on demersal fish include data on the mobile epibenthic invertebrates.

As most fish and epibenthic crustaceans are highly mobile and perform seasonal migrations, obscured by the use of annual means, it is not surprising that the spatial structure found is relatively weak (low eigenvalues). Still, there is a remarkably strong similarity between the species assemblages found in the present study and those defined by Henderson 1989). This is even more amazing if one considers the fact that Henderson's data were collected from the intake screens of powers stations, whilst ours were collected by beam trawl. It is also evident that many of the environmental variables that correlate strongly with the structure of the respective communities are related to 'exposure' in a broad sense. Sediment structure (median grain size and mud content, macrobenthic biomass and wave height either directly or indirectly reflect the hydrodynamics of the overlying water (Pearson & Rosenberg 1987) and have been shown to affect settlement of postlarval fish (Pihl & van der Veer 1992, Chapter 4-Add.) and the efficiency of antipredator behaviour (Tallmark & Evans 1986). Henderson's 'exposed estuarine' assemblage consists of three species associations that can be found in virtually the same configuration in the plot of the first two principal components (Fig. 2.15). Some species can be found in close association in both studies, *e.g.* hooknose (*Agonus cataphractus*), cod (*Gadus morhua*) and *T. luscus*. Similarly Henderson's 'sheltered estuarine' assemblage, characterized by *D. labrax*, Mugilidae species and sea snail (*Liparis liparis*) corresponds to the WS cluster. Two of the species in Henderson's 'sheltered marine' assemblage: *Atherina boyeri* and *G. niger* are typical for the Oosterschelde cluster (considering that the present study classifies all sandsmelts as *A. presbyter*, but see Creech 1991). Within the 'exposed marine' assemblage of Henderson there is some disagreement between the two studies. Whilst *A. tobianus* and *T. vipera* are common to both Henderson's 'exposed marine' assemblage and the VX cluster, his assemblage contains a host of other species typical for the VIO and VIG clusters. According to P. Henderson (pers. comm.) this is probably due to the fact that no power stations have been built at truly exposed marine sites of the kind occurring in the seaward part of the Voordelta. The highly dynamic, low macrobenthic biomass sands in VX are ideal for burrowing fishes that do not depend on macrobenthos for their food. The planktivorous sandeels need well oxygenated sands in which rapid burrowing is possible to avoid predators (Macer 1966). *T. vipera* is a sit-and-wait predator that burrows to avoid detection by its preferred prey *Pomatoschistus* species (Creutzberg & Witte 1989) which are quite abundant in that area. The close association of *P. lozanoi* to the negative side of the third axis is not due to a clear preference for the exposed sites but is mainly caused by its conspicuous rarity in the Oosterschelde. In contrast to its close relative *P. minutus* it does not seem to be able to establish itself in the Oosterschelde. In summer, when the small juvenile *P. lozanoi* enter the Oosterschelde, water transparencies are at their maximum (often over 4 m Secchi disk depth), they are presumably very effectively eliminated by visual predators such as *T. luscus* (Chapter 7-Add.) and *P. minutus* (O. Hamerlynck, unpublished data).

From both studies it appears that inshore marine and estuarine fish communities are strongly structured by their environment. When more data will become available it seems likely that, given a number of important characteristics such as latitude, sediment type, current velocities, wave impact and salinity, quite accurate predictions could be made on the type of fish assemblage expected at a certain site. It is therefore recommended that such environmental variables be recorded when sampling demersal fishes and mobile epifaunal invertebrates. Deviations from the expected assemblage could therefore be indicators of special circumstances either in the positive or in the negative sense.

In the positive sense the richness of the VIG assemblage is probably a result of recent changes in the ebb-tidal delta of the former Grevelingen estuary. Since the closure of that estuary in 1971, changes in the current patterns have turned the area into a sink which traps mud, detritus and larvae of fishes, decapods and macrobenthic animals (Chapter 4-Add.). It does not necessarily follow that there is a causal relationship between macrobenthic biomass, or any of its covariables, and the occurrence of a certain species assemblage. Still, it is likely that some of the species occurring towards the right end of the species plot, *e.g. L. Limanda*, *P. minutus* and *A. rubens*, because of their food preferences, seek actively for localities with a high macrobenthic biomass. The VIO assemblage resembles the VIG assemblage but is less rich. The stations of the VIO assemblage correspond to those parts of the ebb-tidal delta of the Oosterschelde where mud has started to accumulate as a consequence of the reduction in current velocities since the completion of the storm-surge barrier in 1986.

A typical example of a deviation in the negative sense can be seen in the Westerschelde which is completely devoid of the freshwater species that, in other areas, occasionally venture into waters of higher salinity. Other notable absents are the Salmonidae, and especially the smelt *Osmerus eperlanus*, which is very abundant in estuaries with sufficient oxygen (Wharfe *et al.* 1984). Though a beam trawl is not the most efficient device to catch such fishes, a number of anadromous fish species should be much more common than at present. Thus *L. fluviatilis* was only recorded once, of *A. fallax* three individuals were caught in a single haul and in total less than ten Mugilidae were caught. This result is in sharp contrast to their abundance in the Severn (Claridge *et al.* 1986) and two British east coast estuaries (Pomfret *et al.* 1991). In 1989, the annual mean oxygen content measured at the Dutch-Belgian border, only a few kilometres upstream from W14, was below 2.5 mg l^{-1} (Van Eck *et al.* 1991). Marine fishes become severely stressed at oxygen levels of less than 4.5 mg l^{-1} (Poxton & Allouse 1982, Marchand 1993). It is therefore unlikely that important fish concentrations occur upstream of W14. The low oxygen levels in the freshwater part of the Schelde are presumably the prime cause for the near absence of the freshwater and anadromous species. Two other absents are the starfish *A. rubens* and the eelpout *Z. viviparus*. The first species used to be common in the Westerschelde but has virtually disappeared (Van Eck *et al.* 1991). The polychlorobiphenyl- and cadmium-contents of starfish from the Westerschelde which are six times higher than the levels in starfish from the Oosterschelde, seem to affect their reproduction (den Besten 1991). The eelpout, a typical estuarine resident which is common in the Tyne and the Forth (Pomfret *et al.* 1991) is very rare in the Westerschelde. Fry survival in this species is known to be negatively affected by mercury (Jacobsson *et al.* 1986, Essink 1989). Though mercury concentrations in the suspended particulate matter of the Westerschelde have decreased to about one third of their former value over the last decade (Van Eck *et al.* 1991) concentrations in the sediments are still four to twentyfive times higher than North Sea background levels. Similar tests as those performed for starfish could be done with eelpout to prove or disprove this hypothesis.

The second axis in the PCA is clearly influenced by the estuarine gradients in a series of covariables but none of the variables measured has a particularly strong correlation with this second component of the PCA. There are certainly conflicting cost-benefit aspects for fishes inhabiting the brackish part. For species such as *S. sprattus*, *P. minutus* and *P. lozanoi*, which are abundant in the brackish part and are known to feed predominantly on mysids there (Hamerlynck *et al.* 1990 and unpublished data), the important mysid concentrations must be attractive. Avoidance of visual predators in the very turbid inner estuary (Blaber & Blaber 1980) is another bonus for those species. The brown shrimp *C. Crangon* may profit both from the high turbidity and the large supply of detritus from the river. On the other hand, slow moving fish and invertebrates may be subjected to oxygen stress. For flatfish the situation is certainly less than optimal because of the low macrobenthic biomass.

The third axis is very important in the sense that it neatly separates the assemblages defined, except for the subdivision WM-WB. However, except for the stronger correlation with wave height, there is little difference between the environmental biplots for the second and third axes. Some hidden variable *e.g.* current velocity may be structurally important.

2.5 Conclusions

As seen from the results of this study, multivariate statistical techniques have a great potential as a tool for an increased understanding of the structure of natural communities, even of mobile species. Most studies of fishes and fisheries are either based on areas of convenience, *e.g.* the nearest estuary or on statistical rectangles, and these do not necessarily correspond to the extent of natural communities. It would make great biological sense to base functional and process studies on entities which can be distinguished clearly on the basis of their species-abundance composition.

Datasets which can be used for these exploratory studies exist but they often lie idle in the fisheries research institutes. Most often they are only used for the extraction of data on the stock size or on the imminent recruitment of commercially important species. An exception to this rule is the study by Daan *et al.* (1990) which defines three different types of fish community in the North Sea on the basis of a multivariate analysis of the English groundfish survey data. There are many other datasets, covering vastly greater areas than the present study, *e.g.* the ICES Demersal Young Fish Surveys (DYFS) or the 'Aurelia' cruises dataset (Creutzberg 1985) whose spatial and temporal structure could be analysed to great benefit.

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CHAPTER 3 THE MOBILE EPIFAUNA OF THE SOFT BOTTOMS IN THE SUBTIDAL OOSTERSCHELDE: STRUCTURE, FUNCTION AND IMPACT OF THE STORM-SURGE BARRIER

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Key words: spatial community structure, production, soft sediment, mobile epifauna, beam trawl, Oosterschelde estuary

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Abstract. *Data on the mobile epifauna of the Oosterschelde, collected by beam trawl, were compiled from several studies. Multivariate statistical techniques brought out the fact that the Oosterschelde, when compared with neighbouring areas, has a characteristic epibenthic fauna. Diversity as measured by Hill's diversity numbers N_0 through $N_{+\infty}$, is higher for the Oosterschelde ($N_1 = 4.5$) than for the Voordelta ($N_1 = 3.5$) and the Westerschelde ($N_1 = 2.2$). Four epifaunal communities can be distinguished within the Oosterschelde, the two most seaward communities being the richest. Annual production is estimated at about 6 gADW m^{-2} yr^{-1}, annual consumption is estimated at over 25 gADW m^{-2} yr^{-1}. These results are highly dependent on the assumptions. Over 85 % of the epibenthic production and consumption in the Oosterschelde is accounted for by only six species: starfish Asterias rubens, plaice Pleuronectes platessa, bib Trisopterus luscus, brown shrimp Crangon crangon, shore crab Carcinus maenas and dab Limanda limanda. In spite of its abundance, the sand goby Pomatoschistus minutus contributes little to the production. From the available data it is difficult to assess the impact of the construction of the storm-surge barrier and the compartmentalization dams on the epibenthic fauna. The increase in flatfish in the Hammen area is probably linked to the decrease in current velocities in that area. On the other hand the increase in the gadoids bib and whiting Merlangius merlangus is predominantly due to the stronger year classes in the post-barrier time period. Lower nutrient inputs through the Northern branch, in combination with the increase of the gadoids, may have caused the decline of the brown shrimp in the Oosterschelde. A decrease has also been observed in the sandeel Ammodytes tobianus and the hooknose Agonus cataphractus.*

3.1 Introduction

Shallow coastal areas and estuaries are dynamic, productive and economically important aquatic ecosystems (McLusky *et al.* 1978). The high primary productivity and the relatively low grazing activity of the zooplankton are the basis for the importance of benthic heterotrophs in shallow coastal areas (Hannon & Joiris 1989). Several studies have demonstrated the significant role of the mobile epifauna (predominantly consisting of demersal fishes, shrimps, crabs and starfish) in the matter and energy fluxes in shallow marine areas, both in the intertidal (Kuipers *et al.* 1981) and in the shallow subtidal (Evans 1984, Möller *et al.* 1985). Many epibenthic predators have been shown to affect the structure of infaunal communities (review in Wilson 1991).

Though extensive data collection has been done on the epibenthos of the soft sediments (both subtidal and intertidal) in the Oosterschelde over the last ten years, only a limited amount of data are presently available. The data were collected by several research groups for different purposes using different methodologies. Data on the subtidal macrofauna and

on the bottom characteristics at most of the sampling sites are conspicuously absent. This paper can therefore only present a preliminary analysis of the structure and function of the mobile subtidal epibenthos in the Oosterschelde.

To characterize the Oosterschelde, the epibenthic fauna of three localities in the Oosterschelde in 1988 is compared to the fauna in the Westerschelde and the neighbouring coastal area (Voordelta). Then the Oosterschelde is analyzed more detailed using the quarterly surveys of 1988 and 1989. The Oosterschelde is divided into four communities on the basis of multivariate statistical methods. Biomass composition in these communities and in the 'entire' Oosterschelde are analyzed. Subsequently production and consumption are estimated for the main epibenthic species.

As a consequence of the construction of the storm-surge barrier and the secondary compartmentalization dams, important changes have occurred in the hydraulics (Vroon 1994), geomorphology (Mulder & Louters 1994) and ecology (Nienhuis & Smaal 1994b) of the Oosterschelde. An attempt is made to evaluate the impact of the construction works on the mobile epibenthos of the Oosterschelde.

3.2 Material and methods

3.2.1 Sampling

All samples were taken from the R.V. Luctor (34m, 500 Hp) using a 3 metre beam trawl, equipped with a 6 metre long net, a tickler chain and a chain in the groundrope. Trawling was always done with the tide parallel to the depth contours at 5 to 20 m below NAP (approximately Mean Tidal Level). Trawls were approximately 1000 m in length: trawling started from a buoy or other fixed marker and the distance covered was read from the radar screen.

Standard length (SL) was recorded for all epibenthic fish specimens. Invertebrates were counted and (wet)weighed. Net efficiency was assumed to be 20 % for all size classes of fish and epibenthic invertebrates, regardless of mesh size in the cod end. The lower size limit for fishes is approximately 30 mm SL. The Echinodermata Crinoidea were considered to be sessile animals. Therefore starfish *Asterias rubens* were the only echinoderms quantified. Amongst the crustaceans caught, only postlarval shrimp and crabs were quantified. A number of crabs typical for hard substrates such as *Macropodia rostrata*, *Liocarcinus arcuatus* and *L. puber*, and rare shrimps such as *Crangon allmani* and *Pandalus montagui* were occasionally noticed but not quantified. The species *Pagurus bernhardus* is common but was not quantified.

Biomass was calculated from the size-frequency distributions using length - Ashfree Dry Weight (ADW) regressions for fish and wet weight - ADW conversions for the invertebrates (see Tables 4.2 and 5.2).

3.2.2 The Oosterschelde in comparison with neighbouring areas

From November 1987 to December 1988 fortnightly beam trawl samples, using a 5*5 mm mesh in the cod end, were taken at three localities (Fig. 3.1) in the central part of the Oosterschelde (OEV = 20 in Fig. 3.1, OKT = 15 and OWD = 19), with 3 trawls per locality (*e.g* OEV1, OEV2 and OEV3). From January to December 1989 the sampling frequency was halved to a monthly basis, but one locality was added (see section 1.6).

Only the fortnightly samples from May to December 1988 could be used for comparison with neighbouring areas. In this time period monthly samples were taken at 14 localities in the Westerschelde (W1 to W14) and 12 localities in the Voordelta (Fig. 3.1). In the Voordelta each locality represents two stations, one in the gully at NAP -10 m (*e.g* V1G), the other at NAP -5 m on the sandbank slope (*e.g* V1B).

In order to characterize the fish fauna of the Oosterschelde in relation to the neighbouring areas a Correspondence Analysis (CA) (Jongman *et al.* 1987) and a Two Way Indicator Species Analysis (TWINSPAN) (Hill 1979) were performed on the average densities (N per 1000 m^2) of fish and epibenthic invertebrates per station, after a variance-stabilizing 4^{th} root transformation (Field *et al.* 1982). Cut-levels for the TWINSPAN were 0, 0.75, 0.98,

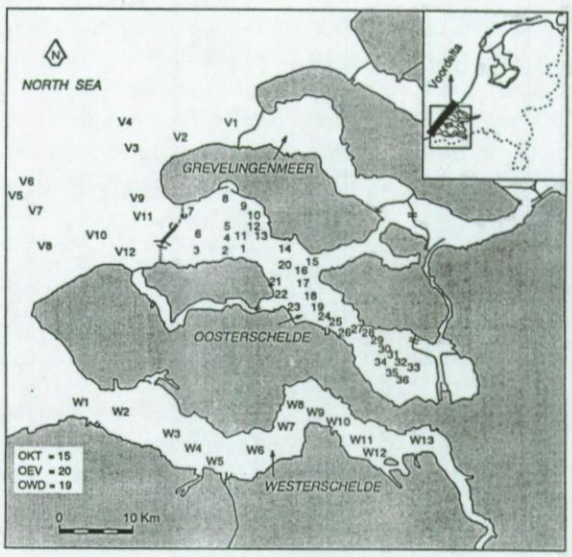

Fig. 3.1 Study area with the sampling localities for the different datasets. The quarterly surveys were taken in the Oosterschelde at numbers 1 through 36. The fortnightly localities in the Oosterschelde OKT, OEV and OWD correspond with the numbers 15, 20 and 19 respectively

1.25, 1.74, 2.65 and 7. These were chosen in order to distribute the number of density values equally among the cut-levels. More details on the methodology of the multivariate statistical techniques are given in Chapter 2-Add.2.

Diversity within the communities, as defined by the CA, was calculated using Hill's diversity numbers of the order 0, 1, 2 and $+\infty$ (Hill 1973). N_0 is defined as the average number of species per station, N_1 is the exponent of the Shannon-Wiener diversity index, N_2 is the reciprocal of Simpson's dominance index and $N_{+\infty}$ is equal to the reciprocal of the proportional abundance of the commonest species (Heip *et al.* 1988).

3.2.3 Spatial community structure within the Oosterschelde

Between June 1983 and November 1989 22 surveys of the epibenthos of the subtidal Oosterschelde were undertaken. Only the 8 surveys conducted in 1988 and 1989 were available at the moment of this study for the analysis of spatial structure (see section 1.6). These surveys covered 36 stations spread out in a more or less regular way (Fig. 3.1). Samples were taken with a 10*10 mm mesh in the cod end. Per station average density and biomass were calculated combining the eight surveys. The 4^{th} root transformed biomass data were used as input for a TWINSPAN. Seven cut-levels were used: 0, 0.21, 0.37, 0.71, 1.31, 2.35 and 5.

3.2.4 Annual production and consumption

Annual production for all species was calculated on the basis of a P/B ratio = 2.5. Because of the important differences between the subareas defined in the community analysis, annual mean biomass was calculated per subarea from the quarterly surveys (July 1988 through May 1989). Annual production for the 'entire' Oosterschelde was then calculated using the proportional extent of these subareas.

A P/C ratio of 0.3 for fish and 0.2 for crustaceans (Pihl 1985) was used to estimate annual consumption of the epibenthos from the production estimates. For starfish the P/C ratio for crustaceans was used.

3.2.5 Changes in the epibenthos of the Oosterschelde: a comparison between 1984-1985 and 1988-1989

To evaluate the impact of the construction of the storm-surge barrier and the compartmentalization dams on the epibenthos, a pairwise comparison using Wilcoxon's signed rank test for two groups was performed (Sokal & Rohlf 1981). The two groups consist of five quarterly surveys from the period 1984-1985 and five surveys from the period 1988-1989. These were selected from all available surveys on the basis of the fact that they were conducted at similar temperatures. Thus July 1984 (16.4 °C) was paired to July 1988 (17 °C), September 1984 (14.7 °C) to September 1988 (15.4 °C), etc. This pairing was deemed necessary because, in a study of the temporal and spatial structure of the mobile epifauna in the neighbouring Voordelta, temperature was shown to be a dominant factor that strongly affected community structure (Arellano 1991). Input was the average biomass per species or taxonomic group from the ten quarterly surveys selected. The analysis was done both for the 'entire' Oosterschelde and for the separate subareas.

3.3 Results

As it is the case for other estuarine and shallow coastal areas, the mobile epifauna makes use of the Oosterschelde in a varied way. Most species can be assigned to one of six categories (Costa & Elliott 1991): estuarine residents *i.e.* species completing their life cycle entirely within estuaries, marine juvenile migrants (MJ) that use the area as a nursery, marine seasonal migrants (MS) whose adults make seasonal incursions into estuaries, marine occasional species (MO), fresh water occasional species (FW) and catadromous and anadromous species (CA). The species quantified in this study have been assigned to these categories in Table 3.2. For the purpose of this paper the conventional category 'estuarine resident' was converted into Oosterschelde resident (OR), because the Oosterschelde is not a true estuary any more and some of the OR species are not typical estuarine species. There is some degree of arbitrariness in the assignment of species to some of the categories. Most of the epibenthic MJ species enter the Oosterschelde as larval planktivorous animals in spring, become benthivorous after metamorphosis and leave the Oosterschelde as adults or subadults in winter. Some individual subadults stay in the Oosterschelde for one or more years, others that have left can have a regular cycle of entering and leaving the Oosterschelde until they reach maturity. The adults can afterwards be either seasonal or occasional visitors. The ecological types followed by a question-mark refer to species whose exact category is still in doubt.

3.3.1 The Oosterschelde in comparison with neighbouring areas

The Oosterschelde has a characteristic epibenthic community in comparison to neighbouring areas. In the plot of the sample scores of the Correspondence Analysis (Fig. 3.2) for the first two axes (eigenvalues 0.11 and 0.11) the six Oosterschelde

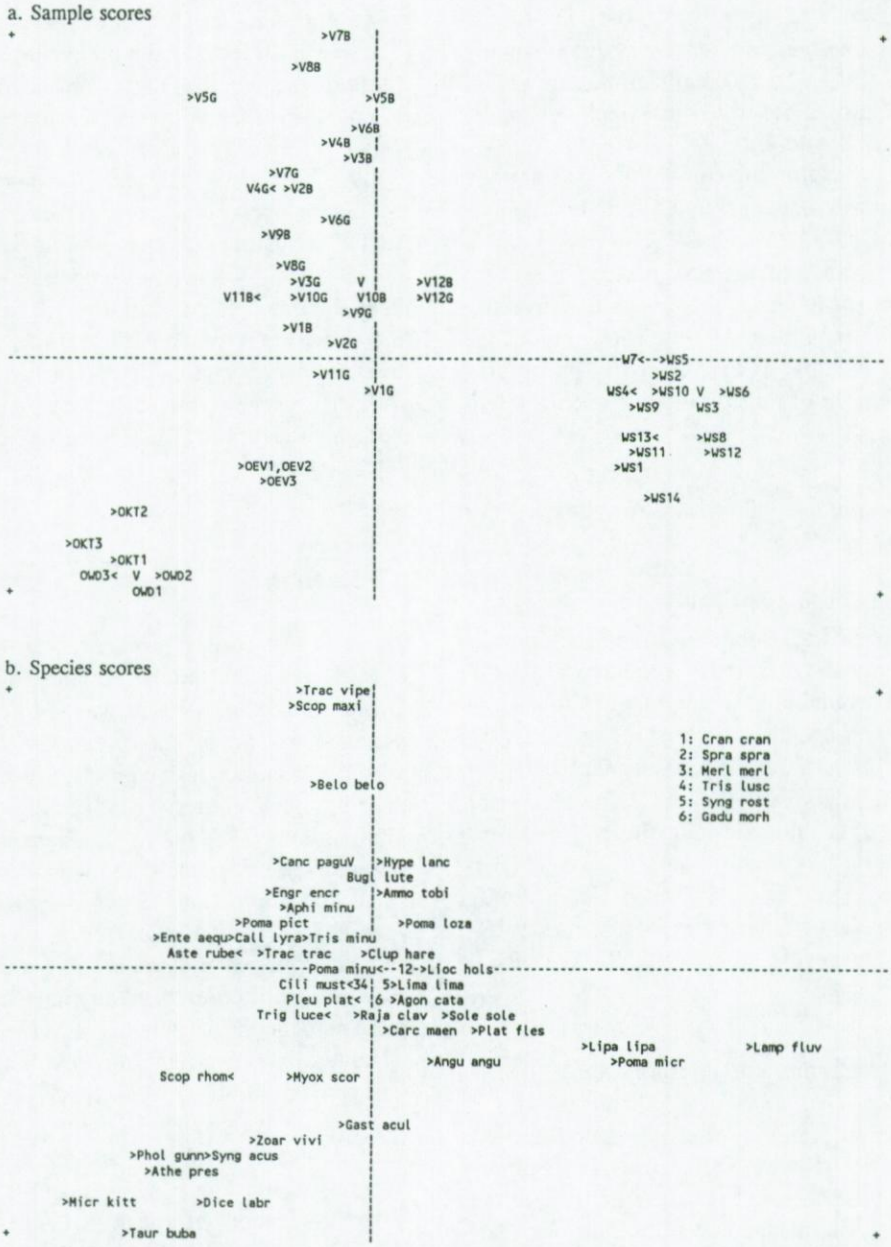

Fig. 3.2 Result of the Correspondence Analysis: sample (a) and species (b) scores in the plane of the first two axes. Species names are abbreviated to four letters of the genus name followed by four letters of the species name

stations from the OWD and OKT localities form a separate subgroup towards the lower left. The three stations from the locality closest to the mouth (OEV) take up an intermediate position between this subgroup and the origin. The two other areas also form distinct clusters, the Westerschelde cluster along the first (horizontal) axis and the Voordelta cluster along the second. From the species plot (Fig. 3.2) it is clear that this structure is linked to the presence of a few characteristic species in the Oosterschelde, *i.e.* the sea scorpion *Taurulus bubalis* Euphrasen 1786, the lemon sole *Microstomus kitt* Walbaum 1792, the sand smelt *Atherina presbyter* Cuvier 1829, the sea bass *Dicentrarchus labrax* Linnaeus 1758, the butterfish *Pholis gunnellus* Linnaeus 1758, the greater pipefish *Syngnathus acus* Linnaeus 1758, the eelpout *Zoarces viviparus* Linnaeus 1758, the stickleback *Gasterosteus aculeatus* Linnaeus 1758, the bull-rout *Myoxocephalus scorpius* Linnaeus 1758 and the brill *Scophthalmus rhombus* Linnaeus 1758.

The TWINSPAN (Fig. 3.3) classifies the nine Oosterschelde stations (community OS) with eight stations from the Voordelta (community VD A). This cluster, together with the cluster containing the Westerschelde stations (community WS) are separated from the cluster containing all the other Voordelta stations (community VD B). As in this paper we are mainly interested in the Oosterschelde we have lumped the two Westerschelde communities (within WS) and the two Voordelta communities

Table 3.1 Average abundance (numbers per 1000 m²) for the four communities as defined by Twinspan, ranked according to abundance for the Oosterschelde community. OS = Oosterschelde; VD A = Voordelta A; VD B = Voordelta B; WS = Westerschelde

Species	Community			
	OS	VD A	VD B	WS
Asterias rubens Linnaeus 1758	1400	890	360	–
Crangon crangon L. 1758	380	6200	1100	2300
Pomatoschistus minutus Pallas 1769	140	710	65	130
Pleuronectes platessa L. 1758	80	100	10	10
Limanda limanda L. 1758	60	540	30	110
Carcinus maenas L. 1758	45	30	2	15
Clupea harengus L. 1758	20	25	15	4
Trisopterus luscus L. 1758	20	60	6	4
Liocarcinus holsatus Fabricius 1798	10	320	40	160
Merlangius merlangus L. 1758	7	35	3	1
Callionymus lyra L. 1758	6	6	4	–
Syngnathus rostellatus Nilsson 1855	6	11	2	5
Zoarces viviparus L. 1758	4	0.4	–	0.1
Pomatoschistus lozanoi de Buen 1923	4	560	100	100
Myoxocephalus scorpius L. 1758	4	0.6	0.1	0.1
Sprattus sprattus L. 1758	4	4	3	9
Ammodytes tobianus L. 1758	3	1	21	2
Solea solea L. 1758	1	35	0.8	9
Gadus morhua L. 1758	0.9	4	0.4	0.6
Syngnathus acus L. 1758	0.8	–	<0.1	0.1
Agonus cataphractus L. 1758	0.5	35	1	1
Pholis gunnellus L. 1758	0.5	0.6	–	–
Trigla lucerna L. 1758	0.5	0.1	0.1	0.1
Microstomus kitt Walbaum 1792	0.4	–	–	–
Gasterosteus aculeatus L. 1758	0.3	–	–	0.1
Scophthalmus rhombus L. 1758	0.3	–	<0.1	–
Pomatoschistus pictus Malm 1865	0.2	1.0	0.4	–
Trachurus trachurus L. 1758	0.2	0.4	0.3	<0.1
Anguilla anguilla L. 1758	0.2	0.5	<0.1	0.4
Hyperoplus lanceolatus le Sauvage 1824	0.2	0.3	0.5	0.1
Atherina presbyter Cuvier 1829	0.2	–	–	<0.1
Aphia minuta Risso 1810	0.1	4	0.5	<0.1
Platichthys flesus L. 1758	0.1	10	0.1	3
Pomatoschistus microps Krøyer 1838	0.1	–	<0.1	3
Entelurus aequoreus L. 1758	0.1	–	<0.1	–
Dicentrarchus labrax L. 1758	0.1	–	–	<0.1
Trisopterus minutus L. 1758	0.1	0.2	0.1	–
Taurulus bubalis Euphrasen 1786	<0.1	–	–	–
Ciliata mustela L. 1758	<0.1	0.1	<0.1	<0.1
Liparis liparis L. 1758	<0.1	1.1	<0.1	1.2
Buglossidium luteum Risso 1810	–	–	<0.1	<0.1
Cancer pagurus L. 1758	–	0.1	0.1	–
Engraulis encrasicolus L. 1758	–	–	<0.1	–
Scophthalmus maximus L. 1758	–	–	0.1	–
Belone belone L. 1758	–	–	<0.1	–
Trachinus vipera Cuvier 1829	–	–	0.5	–
Raja clavata L. 1758	–	0.1	–	–
Lampetra fluviatilis L. 1758	–	–	–	<0.1

(within VD B) that were distinguished at the third level of division. Indicator species for the Voordelta A subcluster, dividing it from the Oosterschelde is Lozano's goby *Pomatoschistus lozanoi* de Buen 1923. Four stations of the VD A community are located in the inner part of the lagoon that has come into being in what was formerly the ebb-tidal delta of the Grevelingen estuary (Louters *et al.* 1991). The other four stations are located in front of the storm-surge barrier. Details on the structure of the epibenthic communities in the other areas will be published elsewhere (Chapter 2-Add.2).

Table 3.1 shows the average densities for the four communities defined by the TWINSPAN. A number of species have similar densities in the VD A and the OS communities and are less abundant in both other communities, i.e. the dragonet *Callionymus lyra* Linnaeus 1758 (indicator species), Nilsson's pipefish *Syngnathus rostellatus* Nilsson 1855 and *P. gunnellus*. Species that are more abundant in the OS

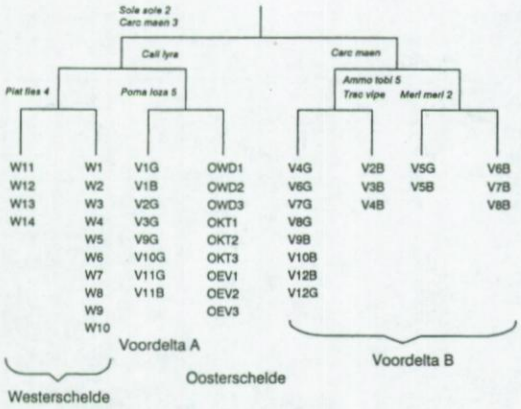

Fig. 3.3 Result of the TWINSPAN on the 4th root transformed density data of the monthly (fortnightly) samples. The indicator species (with cut-levels 1 or given) for each division are abbreviated

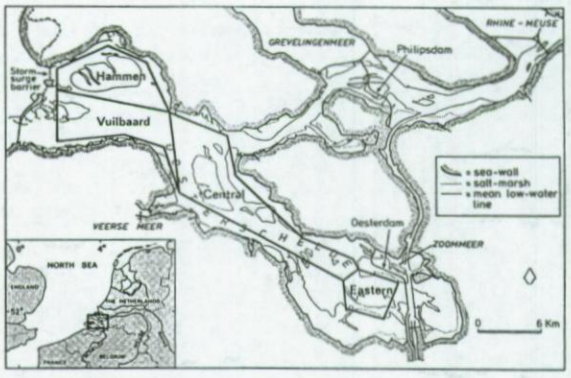

Fig. 3.5 The four mobile epifauna communities in the Oosterschelde estuary as defined by the TWINSPAN

community than elsewhere are the plaice *Pleuronectes platessa* Linnaeus 1758, the shore crab *Carcinus maenas* Linnaeus 1758, the tub gurnard *Trigla lucerna* Linnaeus 1758, the snake pipefish *Entelurus aequoreus* Linnaeus 1758 and the 'characteristic' species as defined in the CA. These species appear as preferentials for the OS cluster in the TWINSPAN. The Oosterschelde stations are poorer than the surrounding areas for the brown shrimp *Crangon crangon* Linnaeus 1758, the swimming crab *Liocarcinus holsatus* Fabricius 1798 and, of course, the 'negative' indicator species *P. lozanoi* (Table 3.1).

3.3.2 Diversity

In the Oosterschelde 40 species were recorded, in the Voordelta 42 species and only 32 species in the Westerschelde. However the average number of species recorded per station for each community (N_0) is significantly higher for the Oosterschelde (29.3 ± 0.7 S.E.) than for the Voordelta (22.5 ± 0.6 S.E.) or for the Westerschelde (21.5 ± 0.4 S.E.). The diversity

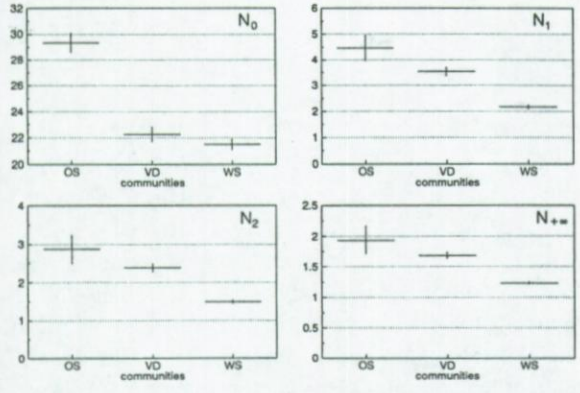

Fig. 3.4 Hill's diversity numbers N_0, N_1, N_2 and $N_{+\infty}$ for the different communities as defined by the CA, mean with Standard Error (S.E.). OS = Oosterschelde; VD = Voordelta; WS = Westerschelde

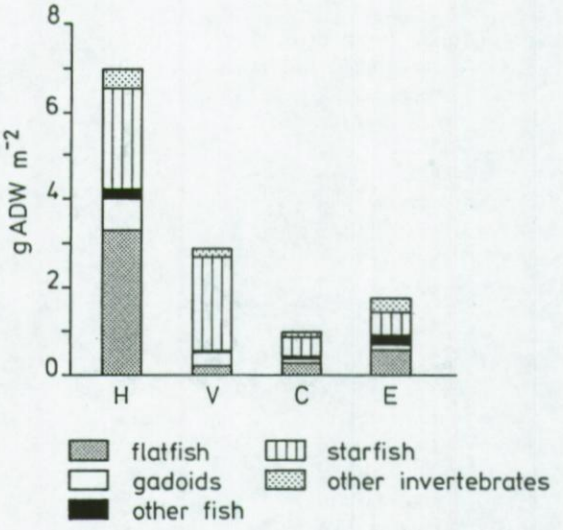

Fig. 3.6 The four communities as defined by the TWINSPAN (H = Hammen; V = Vuilbaard; C = Central; E= Eastern) with the annual mean biomass composition per community

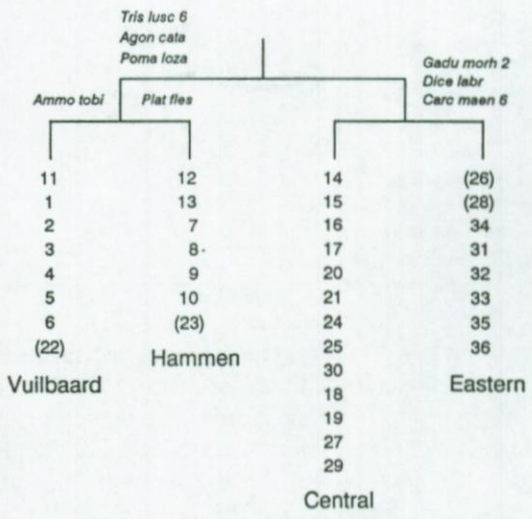

Fig. 3.7 Result of the TWINSPAN on the 4th root transformed biomass data of the quarterly surveys. The indicator species (with cut-levels 1 or given) for each division are abbreviated as in Fig. 3.2. Numbers represent sampling localities in Fig. 3.1

numbers of higher order show the same pattern as N_0, but as the influence of species richness decreases with increasing order, the values for the Voordelta come closer to these of the Oosterschelde (Fig. 3.4). Hill's N_1 f.i. is 4.5 (± 0.5 S.E.) for the Oosterschelde, 3.5 (± 0.2 S.E.) for the Voordelta and 2.2 (± 0.1 S.E.) for the Westerschelde.

3.3.3 Spatial structure in the subtidal of the Oosterschelde

The TWINSPAN classifies the epibenthic fauna of the Oosterschelde into 4 communities (Fig. 3.5 and Fig. 3.6). Two communities (Vuilbaard & Hammen) in the western part, a commmunity (Central) corresponding to the central part and a community (Eastern) corresponding to the eastern part. Four stations (23, 24, 26 and 28) do not conform to the general geographical pattern and are not used for further analyses. Relative surface areas for these communities are: Hammen 22 %, Vuilbaard 28 %, Central 40 % and Eastern 10 %.

Indicator species for the two western communities are the bib *Trisopterus luscus* Linnaeus 1758, the hooknose *Agonus cataphractus* Linnaeus 1758 and *P. lozanoi*. Other indicator species are the sandeel *Ammodytes tobianus* Linnaeus 1758 for the Vuilbaard, the flounder *Platichthys flesus* Linnaeus 1758 for the Hammen and cod *Gadus morhua* Linnaeus 1758, *D. labrax* and *C. maenas* for the Eastern community (Fig. 3.7).

Table 3.2 gives the biomass composition for the different communities and for the 'entire' Oosterschelde. More than 80 % of the average biomass of 2.5 gADW m^{-2} in the subtidal Oosterschelde is formed by only five species i.e. starfish *Asterias rubens* Linnaeus 1758 (1 gADW m^{-2}), *P. platessa* (0.6 gADW m^{-2}), *T. luscus* (0.2 gADW m^{-2}), dab *Limanda limanda* Linnaeus 1758 (0.15 gADW m^{-2}) and *C. crangon* (0.1 gADW m^{-2}). Adding the next seven species, i.e. *C. maenas*, *M. scorpius*, eel *Anguilla anguilla* Linnaeus 1758, *Z. viviparus*, sole *Solea solea* Linnaeus 1758, whiting *Merlangius merlangus* Linnaeus 1758 and *P. flesus*, more than 96 % of the biomass is accounted for.The faunal composition of the four communities shows that the Hammen community is much richer than the other three communities (Fig. 3.6). This is reflected in the highest biomass for the top 14 species in the ranking for the 'entire' Oosterschelde with the exception of *C. maenas* and *M. scorpius*, two species that have their highest biomass in the Eastern community (Table 3.2).

The Vuilbaard community is the second richest one but supports only about 40 % of the biomass of the Hammen community. A number of spe-

Table 3.2 Average biomass (gADW per 1000m^2) for the four communities as defined by Twinspan, ranked according to biomass for the 'entire' Oosterschelde. For the explanation of the ecological types, see text

Species	Community					
	Hammen	Vuilbaard	Central	Eastern	Entire	Type
Asterias rubens	2300	2100	410	470	1050	OR
Pleuronectes platessa	2500	150	210	360	610	MJ
Trisopterus luscus	330	200	60	95	160	MJ
Limanda limanda	510	40	70	95	150	MJ
Crangon crangon	285	140	55	60	110	OR
Carcinus maenas	100	25	50	260	90	OR
Myoxocephalus scorpius	95	15	35	110	65	OR
Anguilla anguilla	115	30	7	40	40	CA
Zoarces viviparus	170	5	9	6	35	OR
Solea solea	80	35	10	40	30	MJ
Merlangius merlangus	100	40	7	7	30	MJ
Platichthys flesus	90	4	5	55	30	CA
Gadus morhua	60	35	2	6	20	MJ/MO?
Liocarcinus holsatus	50	25	10	3	20	MS/OR?
Clupea harengus	8	0.7	7	35	15	MJ
Pomatoschistus minutus	8	7	5	30	10	OR
Sprattus sprattus	1	3	5	40	9	MJ
Callionymus lyra	7	0.8	2	3	3	MS
Ammodytes tobianus	–	3	4	0.3	2	OR
Scophthalmus rhombus	–	–	3	3	2	MO/OR?
Trigla lucerna	5	0.9	1	–	1	MJ
Ciliata mustela	3	–	0.8	2.0	1	MS
Trisopterus minutus	3	1	0.1	1	1	MO
Microstomus kitt	–	–	1	0.8	0.9	MO/OR?
Syngnathus acus	0.9	0.1	1	1	0.8	OR
Agonus cataphractus	2	0.5	0.3	0.0	0.6	OR
Dicentrarchus labrax	–	–	0.4	3	0.6	MJ
Pholis gunnellus	2	–	0.1	1	0.5	OR
Hyperoplus lanceolatus	–	–	0.8	–	0.3	MO/OR?
Entelurus aequoreus	–	0.4	–	–	0.1	MO/OR?
Trachurus trachurus	–	<0.1	0.3	–	0.1	MJ/MS
Taurulus bubalis	–	0.2	0.1	0.1	0.1	OR
Gobius niger L. 1758	–	–	–	0.4	0.1	OR
Syngnathus rostellatus	0.1	<0.1	0.1	<0.1	0.1	OR
Gasterosteus aculeatus	<0.1	<0.1	0.1	<0.1	<0.1	FW/OR
Liparis liparis	–	–	<0.1	0.1	<0.1	OR
Pomatoschistus lozanoi	0.1	0.1	<0.1	–	<0.1	MJ
Pomatoschistus microps	<0.1	<0.1	<0.1	<0.1	<0.1	OR
Atherina presbyter	<0.1	–	–	–	<0.1	OR
Aphia minuta	–	>0.1	–	–	<0.1	MO
Sum	6800	2800	970	1700	2500	

cies have their highest biomass in the two westernmost communities, *i.e. A. rubens*, *C. crangon*, *M. merlangus*, *L. holsatus*, poor cod *Trisopterus minutus* Linnaeus 1758 and, of course, the indicator species for these two communities, i.e. *T. luscus*, *A. cataphractus* and *P. lozanoi*.

The biomass composition of the Central (and poorest) community is rather similar to the ranking for the total Oosterschelde. Very few species reach their highest biomass in this community, none of which is in the top 15 for the Oosterschelde. The species are *A. tobianus*, the greater sandeel *Hyperoplus lanceolatus* le Sauvage 1824, *S. rhombus*, *M. kitt* and scad *Trachurus trachurus* Linnaeus 1758.

The Eastern community supports the highest biomass of *C. maenas*, *M. scorpius*, herring *Clupea harengus* Linnaeus 1758, sprat *Sprattus sprattus* Linnaeus 1758, sand goby *Pomatoschistus minutus* Pallas 1769, black goby *Gobius niger* Linnaeus 1758 and sea-snail *Liparis liparis* Linnaeus 1758.

3.3.4 Annual production and consumption

The annual production of the epibenthic fauna of the Oosterschelde, using a P/B ratio of 2.5, amounts to about 6 gADW m^{-2} yr^{-1} in the production year July 1988 - May 1989 (Table 3.3). This would represent a consumption of more than 25 gADW m^{-2} yr^{-1}.

More than half of the total production is formed by the invertebrates of which the largest share (3 gADW m^{-2} yr^{-1}) is accounted for by the starfish. Flatfish produce the bulk (70 %) of the total fish production, which amounts to 3 gADW m^{-2} yr^{-1}. The fish of the Oosterschelde would consume about 10 gADW m^{-2} yr^{-1}.

The annual production for dab *L. limanda* is estimated to be 0.15 gADW m^{-2} yr^{-1} and consumption about 0.5 gADW m^{-2} yr^{-1}. For plaice *P. platessa* an annual production of 1.9 gADW m^{-2} yr^{-1} leads to a consumption of 6 gADW m^{-2} yr^{-1}. Bib *T. luscus* produces approximately 0.4 gADW m^{-2} yr^{-1} and consumes 1.4 gADW m^{-2} yr^{-1}. For whiting *M. merlangus* annual production and consumption are estimated to be 0.07 gADW m^{-2} yr^{-1} and 0.25 gADW m^{-2} yr^{-1}, respectively. Annual production for sand goby *P. minutus* is 0.02 gADW m^{-2} yr^{-1} and consumption is estimated to be about 0.05 gADW m^{-2} yr^{-1}.

Besides the four invertebrate species, the four most important flatfish species and four gadoids, only *M. scorpius* and *A. anguilla* have important individual productions. Only the top 20 epibenthic species have a production higher than 0.01 gADW m^{-2} yr^{-1}. The sum of the productions of the other 23 species is only 0.02 gADW m^{-2} yr^{-1}.

For almost all species the Hammen subarea has a production per unit area that is much higher than the other subareas, except for a few species like *S. sprattus* and *P. minutus* which have their highest production in the Eastern part or like *G. morhua*, *A. tobianus* and *S. rhombus* which have their highest production in the Central part. The Central part has the lowest productivity. Consumption in the different subareas will naturally reflect the different productivity levels (Table 3.3).

Table 3.3 Annual production and consumption (gADW m^{-2} yr^{-1}) between July 1988 and May 1989 per subarea (H: Hammen, V: Vuilbaard, C: Central and E: Eastern) with P/B = 2.5 and P/C = 0.3 (fish) or 0.2 (invertebrates) ranged according to production in the 'entire' Oosterschelde (OS)

Species	Production					Consumption
	H	V	C	E	OS	OS
Asterias rubens	5.8	4.0	1.2	0.7	2.9	14.5
Pleuronectes platessa	6.7	0.4	0.6	0.8	1.9	6.3
Trisopterus luscus	0.6	0.6	0.2	0.4	0.4	1.4
Crangon crangon	0.7	0.3	0.09	0.04	0.3	1.4
Carcinus maenas	0.3	0.07	0.12	0.7	0.2	0.9
Limanda limanda	0.4	0.06	0.05	0.2	0.15	0.5
Myoxocephalus scorpius	0.2	0.04	0.06	0.09	0.09	0.3
Anguilla anguilla	0.3	0.04	0.01	0.08	0.08	0.3
Merlangius merlangus	0.2	0.09	0.02	0.02	0.07	0.2
Zoarces viviparus	0.2	0.02	0.02	0.01	0.06	0.2
Solea solea	0.15	0.04	0.02	0.05	0.06	0.2
Gadus morhua	0.05	0.15	<0.01	0.02	0.05	0.16
Liocarcinus holsatus	0.14	0.02	0.02	0.01	0.05	0.2
Platichthys flesus	0.13	<0.01	0.01	0.08	0.04	0.14
Sprattus sprattus	<0.01	<0.01	<0.01	0.16	0.02	0.06
Pomatoschistus minutus	0.02	0.02	0.01	0.05	0.02	0.05
Clupea harengus	0.02	<0.01	0.01	0.06	0.01	0.04
Callionymus lyra	0.02	<0.01	0.01	<0.01	0.01	0.03
Ammodytes tobianus	–	0.01	0.01	<0.01	0.01	0.02
Trigla lucerna	0.02	<0.01	<0.01	–	0.01	0.02
Scophthalmus rhombus	–	–	0.01	<0.01	<0.01	0.02
Other fish	0.02	0.01	0.01	0.02	0.02	0.05
Total fish	8.9	1.4	1.1	2.0	3.0	10.0
Total invertebrates	6.9	4.3	1.4	1.4	3.4	17.1
Total epifauna	16.0	5.7	2.5	3.3	6.4	27.1

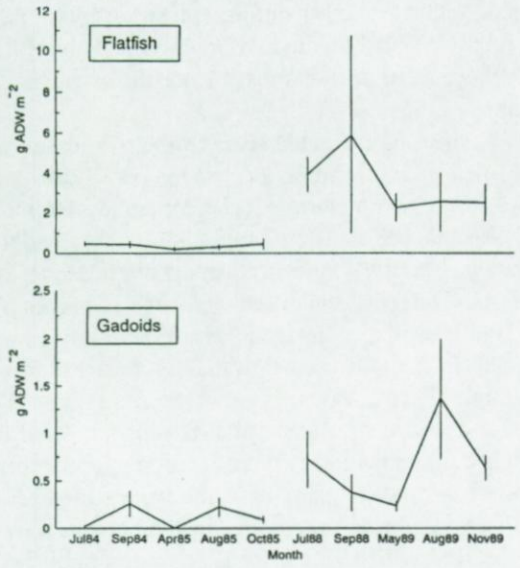

Fig. 3.8 Average biomass per month (± Standard Error) in gram Ashfree Dry Weight per m² for flatfish (top) and gadoids (bottom): a comparison between 1984-'85 and 1988-'89 for the Hammen subarea

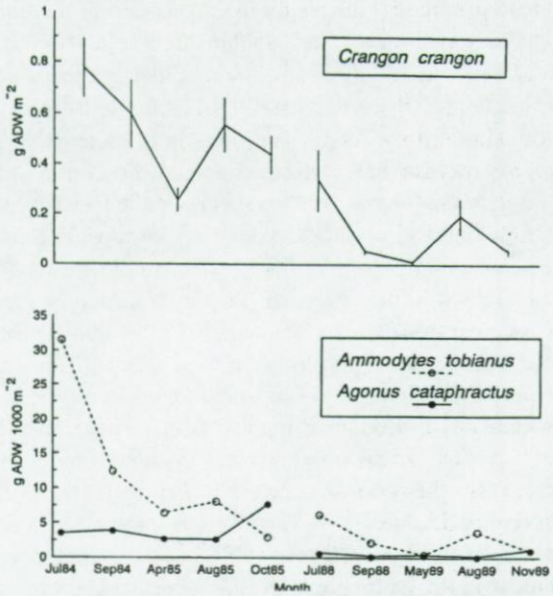

Fig. 3.9 Average biomass per month (± Standard Error) in gram Ashfree Dry Weight per m² for *Crangon crangon* (top) and average biomass per month per 1000m² for sandeel and hooknose (bottom): a comparison between 1984-'85 and 1988-'89 for the 'entire' Oosterschelde

3.3.5 Changes in the epibenthos of the Oosterschelde: a comparison between 1984-1985 and 1988-1989

The pairwise comparison using Wilcoxon's signed rank test for two groups showed a significant increase ($p < 0.05$) in the flatfish and gadoid biomass for the Hammen subarea (Fig. 3.8). The bulk of the flatfish increase is accounted for by plaice *P. platessa* and dab *L. limanda*. Average biomass for plaice increased more than tenfold from 0.2 to 3 gADW m^{-2}. For dab a sevenfold increase from 0.03 to 0.22 gADW m^{-2} was recorded and the biomass for flounder *P. flesus* doubled. The bulk of the gadoid increase is accounted for by bib *T. luscus* and whiting *M. merlangius*. Average biomass for bib increased more than sevenfold from 0.06 to 0.43 gADW m^{-2}, for whiting the increase was about fourfold from 0.03 to 0.13 gADW m^{-2}.

Significant decreases for the total Oosterschelde were found for shrimp *C. crangon*, sandeel *A. tobianus* and hooknose *A. cataphractus* (Fig. 3.9). Average biomass for shrimp decreased fourfold from 0.5 to 0.13 gADW m^{-2}, sandeel decreased fourfold and hooknose eightfold. Many other species showed decreases but these were not significant.

3.4 Discussion

The sampling scheme of the quarterly surveys was less than ideal for a quantification of the epibenthic fauna. In principle stratified random sampling should be the best strategy (Sissenwine *et al.* 1983). Sampling of the subtidal was more or less systematic but limited both in extent (*e.g* the Northern branch was not sampled) and coverage (*e.g* some areas are inaccessible because of construction works, ammunition dumps, mussel culture, etc.). Data from the intertidal stratum have been collected but were not available for this study. Thus estimates for the 'entire' Oosterschelde apply only to the sampled area.

Only few authors did detailed research on net efficiency for beamtrawls (*e.g* Kuipers 1975, Doornbos & Twisk 1984, Rogers & Lockwood 1989). Though there is still high uncertainty about net efficiency for different bottoms (Kuipers *et al.* 1992) there seems to be a strong consensus that the efficiency for demersal fish on 'normal' soft bottoms will be between 20 and 50 % (J.J. Zijlstra, pers. comm.). Elliott & Taylor (1989) use a 33 % efficiency for their study of the fish community of the Forth estuary. For this study an efficiency of 20 % for all length classes of all species was used. This corresponds to the efficiency for flatfish as found by Kuipers (1975). For the immobile starfish the efficiency is probably underestimated and is more likely to be around 50 % (M. Fonds, pers. comm.). Efficiency of a scallop-dredge for starfish was estimated at 44 % (Guillou 1990). Thus the estimates for density, biomass, production and consumption for starfish should be (at least) halved.

The use of diversity indices has been rightfully criticised (review in Washington 1984). Hill's diversity numbers N_0 through $N_{+\infty}$ are useful (univariate) indices of community structure if, when comparing different areas, care is taken that sampling method, sample size, depth of sampling, duration of sampling, time of year and taxonomic level are simi-

lar in all areas (Hughes 1978). Considering the number of trawls performed in the three areas (OS 142, VD 190 and WS 126) and the fact that in the Oosterschelde only three localities, all belonging to the central community, were sampled, it is clear that the Oosterschelde has a diverse epibenthic community. Besides the 'characteristic' species as defined by the CA a number of other typical species were caught when beamtrawling in the Oosterschelde in the following years, i.e. *Dasyatis pastinaca* Linnaeus 1758, *Cyclopterus lumpus* Linnaeus 1758, Mugilidae species, *Raniceps raninus* Linnaeus 1758, *Homarus gammarus* Linnaeus 1758 and *Liocarcinus arcuatus* Leach 1814 (Hostens, unpubl. data). These species, except for *L. arcuatus* which is occasionally observed in the Voordelta, were not recorded from the neighbouring areas. As very little is known on habitat preferences of most of the typical Oosterschelde species it is difficult to explain this exceptional epibenthic fauna. Some of the typical species, such as *T. bubalis* and *P. gunnellus* are dependent on the hard substrates of the Oosterschelde. The rarity of *P. lozanoi* in the Oosterschelde, in comparison with neighbouring areas, is probably linked to the near absence of mysids in the subtidal Oosterschelde (Mees & Hamerlynck 1992). Mysids are the most important prey for this species (Hamerlynck *et al.* 1990).

The importance of pelagic fish is surely underestimated in beamtrawl catches. Still, in shallow coastal areas grazing activity of the zooplankton is relatively unimportant compared to the open sea (Hannon & Joiris 1989). Therefore production of pelagic fish and their predators is unimportant in these areas compared to the production by benthic heterotrophs. Unfortunately there are no data on the macrobenthic fauna of the subtidal Oosterschelde, but the strong dominance of the macrobenthic component, i.e. the molluscs, in the energy fluxes in the Oosterschelde (Herman & Scholten 1990) is probably the basis for the dominance of the demersal macrobenthos feeders in the epibenthos: *i.e.* plaice *P. platessa*, dab *L. limanda*, starfish *A. rubens,* shrimp *C. crangon* and shore crab *C. maenas* (Pihl 1985, Degel & Gislason 1988).

Despite the fact that dab *L. limanda* is the most important demersal fish species in biomass terms in the Southern Bight of the North Sea (Daan *et al.* 1990), only few studies on its biology have been carried out. Dab is restricted to the subtidal for most of its demersal life (Poxton *et al.* 1982). Density and biomass as estimated in this study are therefore more reliable than for species exhibiting strong tidal migrations or for species spending an important part of their life in the intertidal.

The three other abundant flatfish species were surely underestimated. Juvenile plaice *P. platessa* concentrate in the intertidal (van der Veer 1986). Sole *S. solea* prefers muddy substrates and is burried rather deeply during most of the day (Boerema 1964). Flounder *P. flesus* was underestimated because it spends most of its life in the shallow areas.

The Oosterschelde seems attractive to young bib *T. luscus* and whiting *M. merlangus*. These are known to feed on shrimp (Henderson & Holmes 1989, Redant 1982). The biomass is probably underestimated, because length-frequency distributions in catches by line fishermen and in fykes (Chapter 3-Add.) indicate that older gadoids are certainly more abundant in the Oosterschelde than is apparent from the beamtrawl catches.

The use of a general P/B ratio of 2.5 can only yield an indication of possible production levels. There are wide discrepancies in the values found for the different animal groups in the literature (see review by Redant 1989), *e.g* for *C. crangon* published P/B ratios vary from 2 to 9.3. In their study of the Forth estuary Elliott & Taylor (1989) used a P/B ratio of 2.75. Similarly, there is a great need for more accurate estimates of consumption rates in the different groups. Another problem is the fact that the 'annual' production is calculated for only one year and is therefore strongly influenced by year class strength for a number of species.

Annual production (6 gADW m^{-2} yr^{-1}) and consumption (27 gADW m^{-2} yr^{-1}) for the total epibenthos of the Oosterschelde are similar to production (5 gADW m^{-2} yr^{-1}) and consumption (26 gADW m^{-2} yr^{-1}) estimates for the mobile epifauna on the Swedish coast (Möller *et al.* 1985, Pihl 1985). Yet, these results are highly dependent on the assumptions.

Changes in species abundance due to the construction of the storm-surge barrier and the compartmentalization dams have to be evaluated in relation to fluctuations in year class strength (see also Chapter 3-Add.). Year class strengths for plaice have been relatively constant since 1982, with the exception of the strong 1985 yearclass (Rijnsdorp *et al.* 1991). As the bulk of plaice biomass occurring in the beam trawl catches consists of 1+ and 2+ group fish, it is unlikely that the observed increase in the Hammen is due to differences in year class strength for the two time periods. For dab no year class strength data are available, but bycatch data from the Wadden Sea do not show differences in abundance between 1984-85 and 1988 (Tiews 1990). The increase of flatfish (mainly plaice and dab) in the Hammen is probably linked to the decrease in current velocities in this area (Mulder & Louters 1994) with the subsequent sedimentation of silt. As the major changes in current dynamics occurred in the summer of 1985, we must hypothesize the existence of a time lag between these changes and the reaction of the epibenthic community. It also seems logical that the last two surveys of 1985 (August and October) showed no spectacular changes, because most settlement processes for macrobenthic and epibenthic animals

are over by the summer. It could be argued that these last two surveys are not independent of one another because a rich settlement is bound to propagate through all data collected for the rest of that year. The same objection could be brought against the use of both the August and November 1989 surveys. Still, the differences between the two time periods (1984-85 and 1988-89) are so obvious that counting the summer and autumn surveys as only one observation would not have altered the conclusions. In support of the hypothesis, that the increase in the flatfish in the Hammen area is linked to the changed sedimentation pattern, there is the observation from the former ebb-tidal delta of the Grevelingen, where the silting up of the tidal gullies was accompanied by an increased entrapment of passively transported elements like fish eggs and larvae, macrobenthic larvae, detritus, etc. (Hamerlynck & Mees 1991). This created the right conditions for the settlement of rich macrobenthic populations and enhanced the nursery function of the area for flatfish (Chapter 4-Add.).

The gadoids, mainly bib and whiting also increased significantly, but in contrast to the situation for flatfish, this increase is probably not due to the construction works, because gadoid year classes have clearly been stronger in the post-barrier time period (see Chapter 3-Add.).

Sandeel *A. tobianus* and greater sandeel *H. lanceolatus* on the other hand are species typical for dynamic sandy bottoms (Chapter 2-Add.2). The decrease of sandeel with the reduction of current velocities in the Oosterschelde was therefore to be expected. As sandeel are the main prey for brill *S. rhombus* (Braber & De Groot 1973) the decrease in brill (Chapter 3-Add.) may be linked to the decrease in sandeel. There is at present no explanation for the decrease in hooknose *A. cataphractus*. In the bycatch data from the Wadden Sea the hooknose was more abundant in 1985 then in 1984, but no difference was found between 1985 and 1988 (Tiews 1990).

Judging from the Catch per Unit Effort data of the Belgian shrimp fishery (F. Redant pers. comm.) there have been no major changes in shrimp abundance in the Belgian coastal area over the time period studied. The decrease in shrimp *C. crangon* in the Oosterschelde therefore seems to be a local phenomenon and is possibly due to the decrease of nutrient inputs in the Oosterschelde from the river Rhine (Nienhuis & Smaal 1994b) and the associated changes in the phytoplankton (Bakker *et al.* 1990). It was indeed shown by Boddeke *et al.* (1986) that productivity of the brown shrimp in the Dutch coastal area was strongly influenced by nutrient inputs from the Rhine. A second factor in the decrease could be the increased predation pressure from the strong gadoid year classes.

It is a pity that no data are available on the sediment characteristics, current velocities, and macrobenthic biomass at the 36 stations sampled in the quarterly surveys. This would have allowed an analysis of the relationship between the presence of a certain type of fish assemblage and the environment. The changes in these variables as a result of the construction works could have given some indications regarding the possible causes of the observed changes in the mobile epifauna.

3.5 Conclusions

The Oosterschelde has a characteristic and diverse fish community. Four communities can be distinguished within the Oosterschelde, the two most seaward communities being the richest. More than 80 % of the epibenthic biomass in the subtidal is formed by only five species: starfish, plaice, bib, dab and brown shrimp. Annual production is estimated at about 6 gADW m^{-2} yr^{-1}, annual consumption at over 25 gADW m^{-2} yr^{-1}. However these results are highly dependent on the assumptions regarding net efficiency, P/B and P/C ratios. Changes in the current velocities in the Hammen area, which occurred as a consequence of the construction of the storm-surge barrier, are probably the cause for the increase in flatfish in that area. The decreased input of nutrient rich water from the river Rhine through the northern branch of the Oosterschelde is probably the cause for the observed decrease in the brown shrimp in the Oosterschelde. The decrease in sandeel may also be linked to the reduced current velocities in the Oosterschelde.

In future studies much could be gained from the concomitant monitoring of macrobenthic populations and bottom characteristics when monitoring mobile epibenthic animals.

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CHAPTER 3 - ADDENDUM CHANGES IN THE FISH FAUNA OF THE OOSTERSCHELDE ESTUARY - A TEN-YEAR TIME SERIES OF FYKE CATCHES

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Abstract. *Frequency of occurrence of fish species was monitored on a fortnightly basis in four fykes and a weir in the Oosterschelde from 1979 through 1988. This was done in order to record changes in the fish fauna that may have occurred as a response to the construction of a storm-surge barrier in the mouth of the Oosterschelde (1984-1986) and the concomitant building of compartmentalization dams in the landward part. These compartmentalization dams reduced the fresh water inflow into the system. Principal component analysis using the annual averages in frequency of occurrence suggests a slight shift occurred in the fish community separating a cluster of years 1979-1984 from the cluster 1985-1988. Many of the changes in individual species could be attributed to fluctuations in year-class strength or were part of changes occurring on a wider geographical scale. The only impact of the construction works seems to be the decrease in a number of anadromous fish. Fish traps seem to be useful as a monitoring tool for a number of species. The value of the data collected could be improved if catch size and length-frequency data are recorded.*

3.1 Introduction

Fish traps have until recently rarely been used in fisheries research (Hinz 1989). Their suitability for the monitoring of biological effects on the fish fauna has been emphasised by Ruth & Berghahn (1989). If fishing is strictly standardized fykes may also be used for the study of long-term trends in flatfish populations (van der Veer *et al.* 1992).

Fyke nets have the advantage of being relatively unselective (Ruth & Berghahn 1989). They sample demersal fish of stony ground, *i.e.* species that are difficult to catch using towed gears. Fykes also catch pelagic species that are only caught incidentally in a beam trawl (Hinz 1989).

In this study the frequency of occurrence of fish species has been monitored on a fortnightly basis in four fykes and a weir in the Oosterschelde from 1979 through 1988. This was done in order to record changes in the fish fauna that may have occurred as a response to the engineering works in the area. A storm-surge barrier was constructed in the mouth of the Oosterschelde and the building of compartmentalization dams in the landward part reduced the fresh water inflow into the system. In 1984 the impact of the construction works on the hydrodynamics of the system was still very limited. The biggest changes occurred in 1985 and by mid 1987 the new situation was implemented (Nienhuis & Smaal 1994b).

3.2 Materials and methods

Commercial fishermen were asked to monitor the catches of four fyke nets and a weir (see section 1.6) on a fortnightly basis from 1979 through 1988 at dif-

ferent localities in the Oosterschelde (Fig. 3.10). Both types of gear are described in Nédélec (1982).

The four fykes are located close to the dykes and are deployed for catching eel *Anguilla anguilla* Linnaeus 1758. Fykes are emptied on average every three days. Mesh size is 21 mm stretched.

The weir is a traditional fishery directed at the anchovy *Engraulis encrasicolus* Linnaeus 1758. There are two leaders (often several hundred metres long) of stakes set out on an intertidal flat and converging towards the gully. Fish swimming over the shallow areas at high tide are driven towards the chamber in the V-shaped point of the gear when leaving the tidal flat. When the gear is operated actively large schools of anchovy are directed from the chamber into the net attached to the fyke opening of the chamber. Outside the anchovy season and between active catches there is a fyke net attached to this opening and the device functions more or less like a normal fyke net.

A total of 860 samples were used in the analysis. In the summer of 1986 fishing was hampered because of the presence of large quantities of coelenterates in the Oosterschelde. The time series is incomplete for the easterly stations. The locality Zandkreek was only sampled in spring and autumn. There are no data for this station for 1987. Ice floes destroyed the weir during the winters of 1984-1985, 1985-1986 and 1986-1987 and fishing could only be resumed in April.

With the closure of the Oesterdam in the autumn of 1986 the station Bergen op Zoom became part of the Zoommeer. The Zoommeer remained connected rather indirectly to the Oosterschelde through the Philipsdam until April 1987. In the summer of 1987 the Zoommeer became a freshwater lake. Starting in the autumn of 1987 a new locality called 'Oesterbank' was introduced into the monitoring scheme to 'replace' the Bergen op Zoom locality (Fig. 3.10). However the fish fauna caught in the new locality differs substantially from the fauna at Bergen op Zoom. The data for the Oesterdam were thus not included in the analysis. Repeating all the analyses without the time series data for the Bergen op Zoom locality did not affect the results in any substantial way. All species present in the fyke or the weir were noted. The presence of a fish species in each station was expressed as the percentage of catches in which the species occurred (frequency of occurrence) in a single year. The frequency of occurrence data for the five sampling localities as reported by Meyer (1989), were averaged to yield an annual frequency of occurrence for the 'Oosterschelde'. This annual frequency of occurrence was subjected to the correspondence analysis option in the package CANOCO (Ter Braak 1987) in order to quantify total community variation. On the basis of the result of this analysis the same data were subjected to the principal component analysis (PCA) option in CANOCO. The frequency

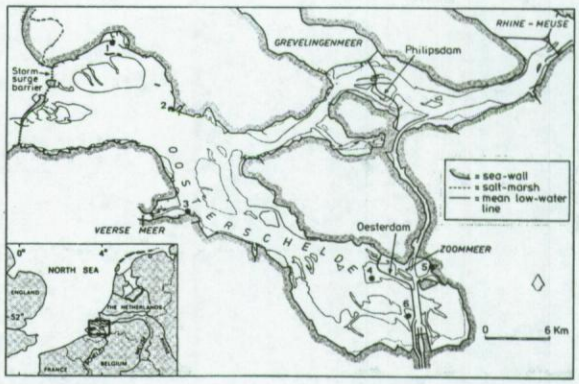

Fig. 3.10 Oosterschelde estuary with sampling localities; 1 = Schelphoek; 2 = Zierikzee; 3 = Zandkreek; 4 = Speelmansplaat (weir); 5 = Bergen op Zoom (until 1986); 6 = Oesterdam (after autumn 1987); Inset: Oosterschelde estuary in The Netherlands on the North Sea

of occurrence data were arc sin transformed for normalisation (Sokal & Rohlf 1981) prior to the PCA. The analysis was repeated after elimination of the species which occurred only in a single year and the species inadequately sampled or difficult to identify. Nilsson's pipefish *Syngnathus rostellatus* Nilsson 1855 and sand goby *Pomatoschistus minutus* Pallas 1769 are too small to be reliably retained and detected in the net. Sand gobies are also liable to predation by larger fish in the catch. Grey gurnard *Eutrigla gurnardus* Linnaeus 1758 was only identified by the fishermen operating the weir. Solenette *Buglossidium luteum* Risso 1810 is rather difficult to identify and may be overlooked in large catches.

A Wilcoxon two sample test (Sokal & Rohlf 1981) was performed on the annual frequency of occurrence data of the individual species to look for significant differences between the clusters of years distinguished along the first PCA axis. For ranking the frequency of occurrence data differences of less than 1 % between years were discarded and indices for those years were considered to be ties.

The product-moment correlation coefficient and Kendall's rank correlation coefficient (Sokal & Rohlf 1981) were calculated between the arc sin transformed frequencies of occurrence and year-class strength indices for a number of species.

3.3 Results

A total of 67 species were recorded (Table 3.4). Ten species occurred on average in more than 50 % of catches, 11 species occurred in 25-50 % of catches, 12 species in 10-25 % of catches, 7 species in 5-10 % of catches and 7 species in 1-5 % of catches. Another 12 species occurred in less than 1 % of catches but were found in at least two years, 9 species were only recorded in a single year.

The correspondence analysis showed that community variation is within a narrow range (less

Table 3.4 List of species caught in the Oosterschelde estuary, ranked according to frequency of occurrence

Species occurring in >50% of catches	
Platichthys flesus Linnaeus 1758	0.96
Anguilla anguilla L. 1758	0.90
Zoarces viviparus L. 1758	0.82
Pleuronectes platessa L. 1758	0.80
Myoxocephalus scorpius L. 1758	0.76
Trisopterus luscus L. 1758	0.66
Clupea harengus L. 1758	0.63
Solea solea L. 1758	0.60
Limanda limanda L. 1758	0.52
Merlangius merlangus L. 1758	0.52
Species occurring in 25–50% of catches	
Gadus morhua L. 1758	0.47
Mugilidae species	0.45
Atherina presbyter Cuvier 1829	0.44
Sprattus sprattus L. 1758	0.40
Dicentrarchus labrax L. 1758	0.38
Belone belone L. 1758	0.38
Trachurus trachurus L. 1758	0.32
Alosa fallax Lacépède 1758	0.31
Syngnatus acus L. 1758	0.28
Ciliata mustela L. 1758	0.27
Pholis gunnellus L. 1758	0.26
Species occurring in 10–25% of catches	
Scophthalmus rhombus L. 1758	0.24
Scomber scombrus L. 1758	0.23
Pollachius pollachius L. 1758	0.21
Cyclopterus lumpus L. 1758	0.20
Engraulis encrasicolus L. 1758	0.18
Agonus cataphractus L. 1758	0.17
Ammodytes tobianus L. 1758	0.16
Trigla lucerna L. 1758	0.15
Gasterosteus aculeatus L. 1758	0.14
Oncorhynchus mykiss Walbaum 1792	0.13
Callionymus lyra L. 1758	0.13
Liparis liparis L. 1758	012

Species occurring in 5–10% of catches	
Entelurus aequoreus L. 1758	0.09
Osmerus eperlanus L. 1758	0.08
Dasyatis pastinaca L. 1758	0.08
Sardina pilchardus Walbaum 1792	0.06
Scophthalmus maximus L. 1758	0.06
Salmo trutta L. 1758	0.05
Taurulus bubalis Euphrasen 1786	0.05
Species occurring in 1–5% of catches	
Pollachius virens L. 1758	0.02
Pomatoschistus minutus Pallas 1769	0.02
Mullus surmuletus L. 1758	0.02
Raniceps raninus L. 1758	0.02
Eutrigla gurnardus L. 1758	0.01
Gobius niger L. 1758	0.01
Petromyzon marinus L. 1758	0.01
Species occurring in <1% of catches	
Lampetra fluviatilis L. 1758	
Conger conger L. 1758	
Microstomus kitt Walbaum 1792	
Syngnathus rostellatus Nilsson 1855	
Spondyliosoma cantharus L. 1758	
Melanogrammus aeglefinus L. 1758	
Galeorhinus galeus L. 1758	
Labrus bergylta Ascanius 1772	
Buglossidium luteum Risso 1810	
Scyliorhinus canicula L. 1758	
Scomberesox saurus Walbaum 1792	
Species recorded only in a single year	
Pomatoschistus microps Krøyer 1838	
Trachinus draco L. 1758	
Squalus acanthias L. 1758	
Crenilabris melops L. 1758	
Arnoglossus laterna Walbaum 1792	
Hyperoplus lanceolatus le Sauvage 1824	
Trisopterus minutus L. 1758	
Balistes carolinensis Gmelin 1789	
Salmo salar L. 1758	

than 1.5 standard deviation units) along the first axis (eigenvalue = 0.03). Thus a linear method (PCA) is more appropriate in this case (Ter Braak & Prentice 1988).

The results of the PCA on the same data are depicted in Fig. 3.11. In the sample plot (Fig. 3.11 bottom) two main clusters can be found in the plane formed by the first two axes (eigenvalues 0.33 and 0.19) with a group 1981-1983 clearly separated from the group 1985-1987 along the first (horizontal) axis. The years 1979 and 1980 are quite far apart within the left upper quadrant of the plane and are clearly separate from the 1981-1983 group along the second (vertical) axis. The year 1984 lies close to the origin. Towards the right of the plane the years 1985-1987 form a rather compact group. The year 1988 lies in the right upper quadrant.

The species plot (Fig. 3.11 top) is the output for the dataset without the species occurring in only a single year and without the inadequately sampled species. The plot with all species is similar except that a number of species around the origin can not be depicted because of lack of space. Species situated around the extremes of the figure along the first axis are the ones which have shown the biggest changes in frequency of occurrence between the years 1979-1984 and the years 1985-1988. Towards the left of the figure (species typical for the years before the barrier impact) are five bearded rockling *Ciliata mustela* Linnaeus 1758, brill *Scophthalmus rhombus* Linnaeus 1758, sardine *Sardina pilchardus* Walbaum 1792, allis shad *Alosa fallax* Lacépède 1758, Mugilidae species (presumably both thick-lipped grey mullet *Chelon labrosus* Risso 1826 and thin-lipped grey mullet *Liza ramada* Risso 1826), sand-smelt *Atherina presbyter* Cuvier 1829, rainbow trout *Oncorhynchus mykiss* Richardson 1836, sea trout *Salmo trutta* Linnaeus 1758, tub gurnard *Trigla lucerna* Linnaeus 1758, lumpsucker *Cyclopterus lumpus* Linnaeus 1758, sea lamprey *Petromyzon marinus* Linnaeus 1758, sprat *Sprattus sprattus* Linnaeus 1758, etc. Towards the right of the figure we find the species typical for the years after the barrier impact: tadpole-fish *Raniceps raninus* Linnaeus 1758, bull-rout *Myoxocephalus scorpius* Linnaeus 1758, saithe *Pollachius virens* Linnaeus 1758, cod *Gadus morhua* Lin-

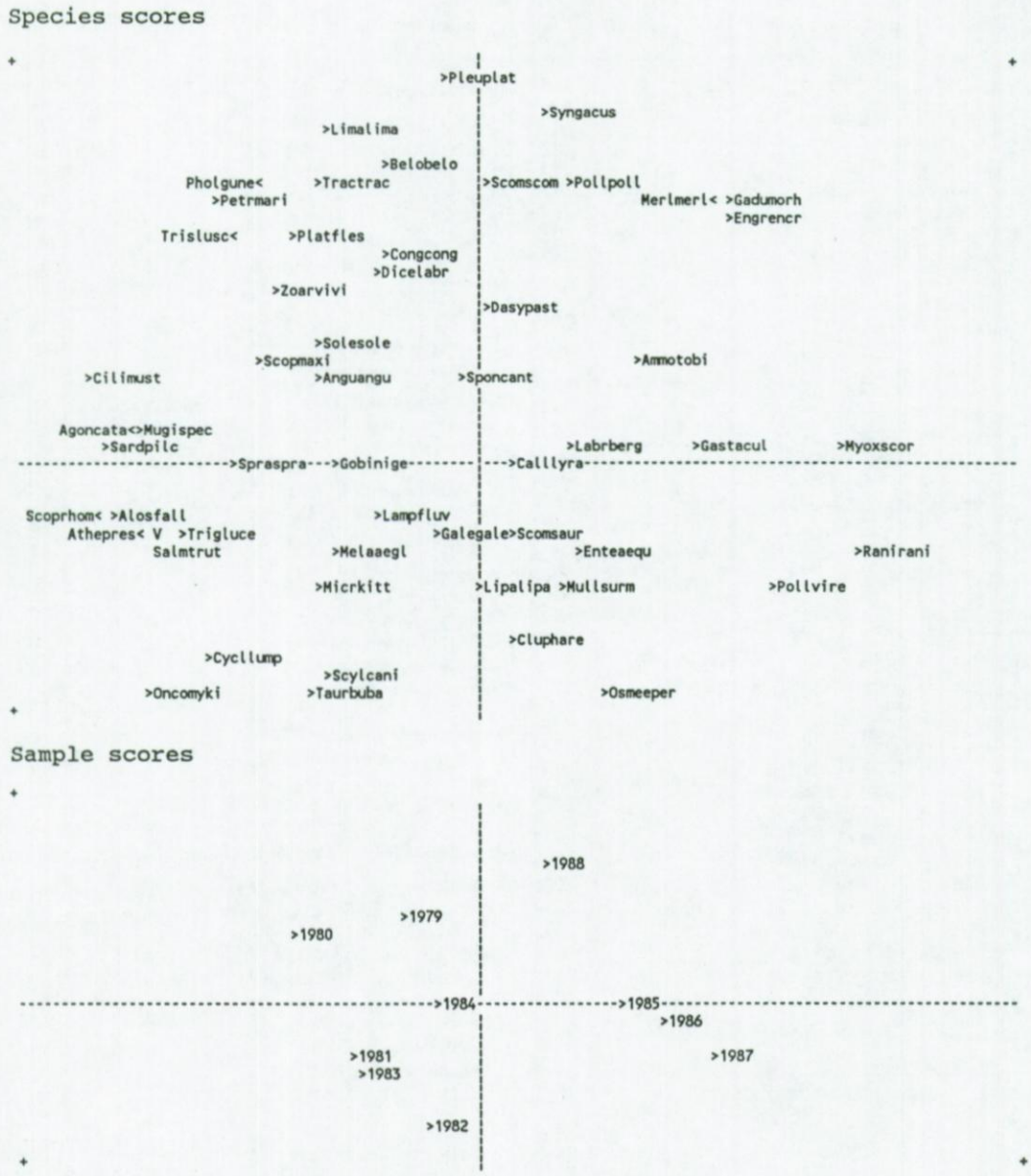

Fig. 3.11 Result of the Principal Component Analysis for the first two axes. Species scores and sample scores are depicted on the same scale. Species names have been shortened to the first four letters of the genus name plus the first four letters of the species name

naeus 1758, anchovy *E. encrasicolus*, whiting *Merlangius merlangus* Linnaeus 1758, three-spined stickleback *Gasterosteus aculeatus* Linnaeus 1758, sandeel *Ammodytes tobianus* Linnaeus 1758, etc.

Significant differences for individual species (Wilcoxon two sample test) between the year blocks as distinguished by the PCA (1979-1984 versus 1985-1988) are shown in Table 3.5. Significant decreases are found for allis shad *A. fallax*, sea trout *S. trutta*, rainbow trout *O. mykiss*, five-bearded rockling *C. mustela*, sand-smelt *A. presbyter*, tub gurnard *T. lucerna*, lumpsucker *C. lumpus*, sand goby *P. minutus* and brill *S. rhombus*. Significant increases are found for cod *G. morhua*, tadpole-fish *R. raninus* and bull-rout *M. scorpius*.

3.4 Discussion

The use of multivariate techniques in ecology is a rather controversial point at present (review in James & McCulloch 1990). We have tried to follow their advice as closely as possible and have only used the techniques as a descriptive tool in an exploratory analysis. Following Jongman *et al.* (1987) we first explored the data using a correspondence analysis (CA), this being a very general (unimodal) model. This gives us the level of variability in the data, which is low, *i.e.* all samples (years) are located within less than 1.5 standard deviations. Ter Braak & Prentice (1988) suggest that non-linear models (like the CA) are inappropriate in these circumstances and

Table 3.5 Results of the Wilcoxon two-sample test for species showing significant differences in frequency of occurrence (FO) between clusters of years as distinguished by PCA

	Average FO 1979–1984	Average FO 1985–1988	
Species with decreased FO			
Alosa fallax	0.38	0.20 **	$p<0.02$
Salmo trutta	0.07	0.02 **	$p<0.02$
Oncorhynchus mykiss	0.18	0.05 *	$p<0.05$
Ciliata mustela	0.33	0.18 *	$p<0.05$
Atherina presbyter	0.51	0.32 *	$p<0.05$
Trigla lucerna	0.19	0.09 ***	$p<0.01$
Cyclopterus lumpus	0.24	0.14 *	$p<0.05$
Pomatoschistus minutus	0.03	0.01 **	$p<0.02$
Scophthalmus rhombus	0.29	0.16 *	$p<0.05$
Species with increased FO			
Gadus morhua	0.38	0.63 **	$p<0.02$
Raniceps raninus	0.01	0.03 *	$p<0.05$
Myoxocephalus scorpius	0.69	0.88 ***	$p<0.01$

linear models (like the PCA) should be used. Following James & McCulloch (1990) we transformed the data for normalisation and used the variance-covariance matrix instead of the correlation matrix. Despite the fact that the Wilcoxon two sample test does not really provide information that is not already apparent from the multivariate analysis it is included in this study because many scientists still feel uncomfortable about the fact that no statistical significance levels are given in the multivariate techniques.

The qualitative dataset, as presently available, is of limited value to describe the changes that occurred in the fish fauna of the Oosterschelde during the construction period. The data can only be used for an exploratory analysis and are certainly not appropriate for any causal investigation. The incompleteness of the time series for the easterly stations may have affected the results.

First of all it is impossible to establish if the fauna caught in the fish traps is in any way representative for the fish fauna of the Oosterschelde. It most certainly cannot be considered to be a random sample: the 5 localities investigated were purposely chosen by the fishermen who, from their experience, selected the best spots to catch either eel or anchovy. Although the fishermen have recorded a crude measure of catch size (1-5, 6-20 and >20) these data were not available for analysis. For some species we know only single individuals were caught, *e.g* allis shad *A. fallax*. As the size of the catches is unknown for all other species the frequency of occurrence is certainly not a measure of fish abundance. Abundant species or species for which the gear is rather selective, i.e. eel *A. anguilla* and flounder *Platichthys flesus* Linnaeus 1758 will be almost always present in the catches and changes in abundance would have to be extremely drastic to become apparent. Eel catches are a case in point. Though the frequency of occurrence has decreased slightly the change is not significant. Both in Britain (Swaby & Potts 1990) and the German Wadden Sea (Tiews 1990) eel catches have been declining in recent years. The same phenomenon has probably occurred in the Oosterschelde as one of the commercial eel fishermen, involved in the sampling scheme, has had to give up because the fishery was no longer profitable. The other fishermen have had to diversify their fishing activities.

Similarly for schooling species like herring *Clupea harengus* Linnaeus 1758 and sprat *S. sprattus* frequency of occurrence seems not to be a sensitive measure for change. It is a well established fact that with the restoration of herring stocks in the North Sea during the 1980's sprat stocks have gone down again to their pre-1970 levels (Garrod 1988, Daan *et al.* 1990). Although a trend in the 'right' direction (increase in herring, decrease in sprat) is recorded in the frequency of occurrence of both species, these trends are not significant.

Catches of the allis shad *A. fallax* always refer to single adult individuals. For this species a change in the frequency of occurrence either reflects a change in phenology, i.e. the season in which the fish is present in the Oosterschelde has expanded or contracted or the change reflects a genuine change in abundance. The significant decrease in frequency of occurrence in *A. fallax* thus probably reflects a true change in abundance linked to the reduction of fresh water inflow in the Oosterschelde (Nienhuis & Smaal 1994b). Decreases in other anadromous species *i.e.* sea lamprey *P. marinus*, lampern *Lampetra fluviatilis* Linnaeus 1758 and sea trout *S. trutta* may have occurred for the same reason.

The changes in frequency of occurrence of both lamprey species are not significant mostly because these species are very rarely caught. This means there are a lot of zeroes in the time series that turn up as ties in the Wilcoxon two sample test. Still, frequency of occurrence is seven times lower for sea lamprey and four times lower for lampern in the years 1985-1988. All four species are rare or vulnerable in most of Northwest Europe because of pollution problems in their riverine habitat and engineering works on their migration routes (Aprahamian & Aprahamian 1990, Swaby & Potts 1990). For the structure and function of the fish community in the Oosterschelde ecosystem the decline in these species is probably unimportant. However, for the species themselves the marginal habitat offered by the Oosterschelde may have been one of their last refuges from which recolonisation of true estuaries, like the Westerschelde, could have originated after the restoration of water quality in these habitats.

A major problem in the interpretation of the observed changes is to distinguish changes possibly linked to the construction works in the Oosterschelde

from natural fluctuations in the size of fish populations over wider areas. This can only be done for species for which we have data on year-class strength or for species for which we have reliable data from other areas. In the German Wadden Sea the bull-rout *M. scorpius* increased in the bycatch of shrimp fisheries from 1970 until 1986. Since then it is on the decline again (Tiews 1990). The increase in frequency of occurrence in the Oosterschelde therefore possibly bears no relationship to the construction works except if the population would remain at the present high level while it is declining elsewhere. From the beam trawl data it appears that *M. scorpius* is much less abundant in 1989 than in the years before (K. Hostens, unpublished data). Similarly the decline in the tub gurnard *T. lucerna* is observed both in the Wadden Sea (Tiews 1990) and the Oosterschelde and may therefore be part of a more general trend in this species.

The rainbow trout *O. mykiss* is not indigenous to the Delta but was introduced into the brackish lake Veerse Meer for 'sports' fisheries. Veerse Meer communicates with the Oosterschelde and the decrease probably reflects population changes in Veerse Meer.

The decrease in frequency of occurrence of the five-bearded rockling *C. mustela* is not matched by a similar decrease in the Wadden Sea. It is a species with a highly variable abundance and has not shown any consistent trend over the past 35 years (Tiews 1990). A longer time series for the Oosterschelde and more information on the ecological requirements of the species are needed to judge if there may have been an impact of the construction works.

For the sand-smelt *A. presbyter* and the lumpsucker *C. lumpus* the decrease in frequency of occurrence does not seem to have a straightforward explanation. Although lumpsucker declined quite strongly in the Wadden Sea during the 1960's the population seems to have stabilised since then, with even a slight increase during the 1980's (Tiews 1990). For the sand-smelt there are no data from the Wadden Sea. Both species and the garfish *Belone belone* Linnaeus 1758, which has also decreased (N.S.), spawn in the Oosterschelde and attach their eggs to algae (Wheeler 1969). If a link exists between the decline in these three species and the construction works it is unclear in what way the impact operated. Needless to say there may be absolutely no link to the construction works, nor any link between the decline in the separate species. One hypothesis may be that the ice floes that moved around the Oosterschelde during the winters of 1984-1985, 1985-1986 and 1986-1987 temporarily damaged the spawning habitat.

For the brill *S. rhombus* no time series for other areas are available. It is therefore difficult to speculate about possible causes.

The increase in the tadpole-fish *R. raninus* seems to be a colonisation phenomenon. The species was first caught in 1982, before the start of the construction works. Initially it was confined to the most seaward stations. It reached the more easterly stations in 1986. It is a species which recently colonised the neighbouring saline lake Grevelingenmeer (Doornbos 1985). The lake communicates with the sea through a sluice which may be the source for the increase in tadpole-fish in the Oosterschelde. Possibly the colonisation was helped by the decreased wave action and the reduced current velocities in parts of the Oosterschelde (Vroon 1994).

For a number of species of commercial fish the Oosterschelde is a nursery area and changes in frequency of occurrence may mainly reflect fluctuations in year-class strength. For several species good estimates of year-class strength for the North Sea covering the time period of this investigation have been published (Rijnsdorp *et al.* 1991). A notable example is cod *Gadus morhua*. This species has clearly increased in the Oosterschelde and at first sight there seems to be no correlation between frequency of occurrence and year-class strength of the same year (Product-moment correlation coefficient r = 0.09, N.S.), nor with year-class strength of the year before (product-moment correlation coefficient r = -0.38, N.S.) (Fig. 3.12). Thus we might conclude that juvenile cod is using the Oosterschelde more intensively since the construction works. An *ad hoc* explanation could then be that the increased transparency of the water is advantageous for visual predators such as cod and whiting. The next step would be to link the decrease in the sand goby *P. minutus*, one of the preferred prey of juvenile cod and whiting (Vea Salvanes 1986) to the increase of their predators. However there is considerable spatial variability in the distribution of the juvenile cod stocks and the strong year-class of 1985 was concentrated in the Southern Bight (Rijnsdorp *et al.* 1991). Thus the high frequency of occurrence in 1985 was probably mainly caused by this phenomenon. Also, in the ab-

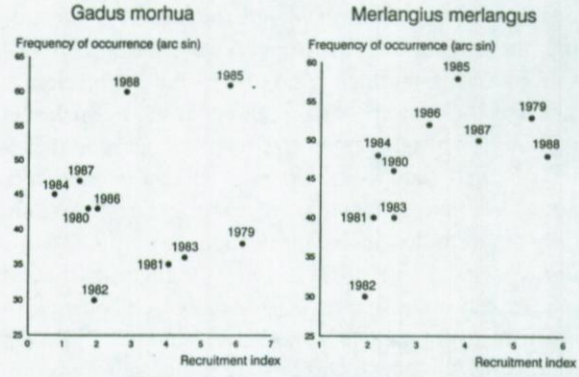

Fig. 3.12 Relationship between year-class strength expressed as a recuitment index (Anonymous 1990) and frequency of occurrence in the Oosterschelde for cod (*G. morhua*) and whiting (*M. merlangus*)

sence of length-frequency distributions of the fish caught, it is impossible to know which year-class is being sampled. From the beam trawl data it appears that small 0-group cod were already present in the Oosterschelde in June 1985 and 1988. In other years, with smaller year-classes it is mainly the 1-group cod that visits the Oosterschelde in winter (Chapter 3). A further complication is due to the fact that the data are at present only available on an annual basis. The 0-group and 1-group cod from a strong year-class affect the frequency of occurrence data of at least two years if they remain present in the Oosterschelde throughout the winter. We believe therefore that the increase in frequency of occurrence in cod is mainly due to the more southerly distribution of recent strong year-classes (1985, 1988). For whiting *M. merlangus* an increase in recent years was suggested by the result of the PCA, though it was not significant in the Wilcoxon two sample test, mainly because of the high frequency of occurrence in 1979 (0.53), the second highest on record. For whiting there is a much better correlation between year-class strength as estimated by the MSVPA (Anonymous 1990) and frequency of occurrence in the Oosterschelde (product-moment correlation coefficient $r = 0.61$, $p < 0.1$, Kendall coefficient of rank correlation $\tau = 0.511$, $p < 0.05$) (Fig. 3.12). For whiting the increase in frequency of occurrence in recent years is thus probably mainly due to the exceptionally poor year-classes from 1981 through 1984.

3.5 Conclusion

The main part of the observed changes in 'community structure' seems to have no relationship to the construction works and the associated changes in the Oosterschelde estuary. Only the decrease in frequency of occurrence of the anadromous fish seems likely to be linked to the decrease of freshwater inflow in the Oosterschelde. Still, catches in the fykes and the weir seem to reflect changes in abundance of many species quite well. The decrease of *A. cataphractus* and *S. rhombus* and the increase of *M. merlangus* were also observed in the beam trawl surveys (Chapter 3). For other species such as *A. tobianus* the two studies have conflicting results. The value of the data recorded by the fishermen would be greatly increased if data on size of the catches and length-frequency distributions could be included. Perhaps this would mean too much work for the commercial fishermen. Separate fish traps owned and operated by research institutes could provide relatively cheap and very valuable data on long-term trends in fish species. Care should be taken to assure that gear, location and operation remain extremely constant in time (see also van der Veer *et al.* 1992). Longer time-series, especially on non-commercial fish species, are an absolute requirement for the assessment of the ecological impact of civil-engineering works or other human activities on the fish community. Baseline studies from many different areas are needed to be able to distinguish natural fluctuations in abundance levels from those caused by man. For example the mere fact that the winters of 1984-1985, 1985-1986 and 1986-1987 were relatively severe may have been important in causing many of the changes observed within the relatively short time period considered here.

For most species it would make good biological sense to analyse the data using a 'year' starting on March 21th. Very few 0-group will occur before that date and few 1-group or older using the Oosterschelde in winter will still be present around that time.

For ecologists it would be a great help if fisheries research institutes could publish time series of abundance indices for all the species they catch in their annual surveys. These data have been collected in a standardized way over extensive areas for about twenty years and could be immensely valuable for the interpretation of local changes.

Analysing the frequency of occurrence data with descriptive multivariate statistical techniques was successful in summarising the structure in the data, thus allowing us to suspect a slight change in community structure after 1984 and pointing out the species that underwent the most important changes.

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CHAPTER 4 THE FISH FAUNA OF THE OOSTERSCHELDE, A DECADE AFTER COMPLETION OF THE ENGINEERING WORKS

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Abstract. *In this study we investigate whether long-term changes in diversity, density and/or biomass of the juvenile fish fauna of the Oosterschelde can be detected. Quarterly beam trawl data from the period 1999-2001 are compared with quarterly data from 1987-89. Also, a brief comparison in frequency of occurrence was made with data from 1960-76. In 1999-2001, a total of 42 fish species was recorded, which is comparable to the period 1960-76. Diadromous species (e.g. Osmerus eperlanus and Anguilla anguilla) showed a reduced frequency of occurrence. Some species (e.g. Gobius niger) still entered the Oosterschelde through sluices, others (e.g. Gasterosteus aculeatus) could not withstand the high salinities in the Dutch Delta area. The number of species per season was 21-28 in 1987-89 and 25-34 in 1999-2001, while the number of species per station was 15-22 in 1987-89 and 17-31 in 1999-2001. This increase could mainly be attributed to rare species. The commonest species in both periods were Pomatoschistus minutus, Pleuronectes platessa, Limanda limanda and Trisopterus luscus. A 45% increase was noted in total average fish density in 1999-2001, which could mainly be attributed to P. minutus. The total average biomass decreased with 35%, but by excluding P. platessa and L. limanda, the decrease was limited to the eastern part in 1999-2001. Both on temporal and spatial scales, density and biomass were significantly different for more than 10 species. Multivariate analyses revealed seasonal (autumn-winter versus spring-summer) and spatial differences (western-central-eastern subareas), with a separation of both periods. For most species the long-term spatio-temporal differences did not reflect 'real' changes in the nursery function of the Oosterschelde. Either they reflected natural population variability due to a delayed appearance of strong yearclasses after cold winters (e.g. high densities of P. platessa and L. limanda in 1987), or changes were obscured through sampling bias (e.g. an increased net-efficiency through clogging of the nets for Syngnathus rostellatus and P. minutus in 1999-2001, or an unexplained reduced efficiency for gobies in 1987-89). For all species with strong yearclasses (also Myoxocephalus scorpius in 1987 and Sprattus sprattus in 1999), the averaged densities rapidly declined to a 'normal' state of homeostasis within the successive years and seasons of both periods. The highest densities were generally recorded in the western and northern part of the Oosterschelde in both periods. Many species (28) showed an increase in the central part. Still, for most species the loss at one station was compensated with an increase at another station in most subareas. This may be related to the location of food resources (e.g. mussels for flatfish in the western part, shrimps for Callionymus lyra in the central part, and high macro- and hyperbenthic biomasses in the northern part). Also, a correlation between substratum type (>50% silt concentration, mainly in the western and northern parts) and high species abundance was observed. For the estuarine resident and marine juvenile species (highest densities of O- and 1-group individuals in summer and autumn) the Oosterschelde can still be considered to be an important nursery area. For several marine seasonal species the ecosystem is still functioning as an important feeding area. Estuarine ecosystems like the Oosterschelde are able to absorb and adjust to changes, but they can also be very vul-*

nerable. One could speak of 'homeostasis' in the fish population in most parts of the Oosterschelde, except in the eastern part where at least 16 species - and especially all flatfish and gadoid species - drastically declined in 1999-2001.

4.1 Introduction

Long time series of biological data are extremely valuable for documenting ecosystem changes and to distinguish between natural and man-induced changes, but they are reversely uncommon as they are expensive and time-consuming to collect (Wolfe *et al.* 1987). A recent study in the German Wadden Sea revealed that the sampling effort to detect 50 to 20% difference in flatfish assemblages between several surveys was disproportionately high (Berghahn 2001). The cost-benefit analysis is reflected in the timescale and the number of stations or subareas that will be monitored. For example, between 1970 and 1975 the Demersal Young Fish Surveys, which are specifically aimed towards flatfish populations as a whole, were undertaken twice per year in the Dutch shallow coastal areas, but thereafter only during fall (Welleman 2000).

It may be difficult and misleading to interpret short-time variations without knowledge of their periodicity and amplitude (Elliott 2002). Weatherhead (1986) found that only a limited number of ecological long-term studies were determined by some unusual event. Due to the large engineering works in the eighties, the Oosterschelde was converted from a real estuary to a marine bay. The present Oosterschelde could be considered a nature reserve of international value, well-balanced between nature, commercial shellfish culture, recreation, and shipping (Wolff 1997; van Berchum & Wattel 1997). The direct consequences on the functioning of the ecosystem during the first years after the works finished in 1987 were reported as the result of an integrated case-study (Nienhuis & Smaal 1994a). For juvenile fish and macrocrustaceans it could not clearly be stated if the changes were directly related to these barriers. For example, flatfish and gadoid densities increased between 1983 and 1989 while shrimp densities decreased. Possible explanations were lower current velocities and stronger year-classes for the fish species and lower nutrient inputs for shrimp (Chapter 3).

On the other hand, monitoring and the detection of man-induced changes need to take into account a background of natural variability (Elliott 2002). On a mid-term scale, primary production in the period 1990-'95 did not differ from the period directly after closure of the Oosterschelde (Wetsteyn 1997). Macrobenthic biomass was a little lower than before 1990, but only locally and if suspension feeders were not taken into account (Stikvoort 1997). Also, a study of non-commercial fish species in the Oosterschelde based on yearly surveys between 1987 and 1995, did not reveal large changes in numbers as compared to the period 1970-'86 (de Jong 1997).

In this study we investigated whether long-term changes in diversity, density and/or biomass of the juvenile fish fauna of the Oosterschelde can be detected. Quarterly beam trawl data on juvenile fish from 1999-2001 (post-barrier period) were compared with data from 1987-'89 (upon completion of the major engineering works) and 1960-'76 (pre-barrier period).

4.2 Material and methods

4.2.1 Study area

The Oosterschelde is a mesotidal marine oligotrophic bay in the Southern Bight of the North Sea, with 227 km² subtidal area and a total area of 351 km² (Fig. 4.1). Typical estuarine gradients have disappeared. Through the construction of the storm-surge barrier (1979-'86) the mean tidal volume decreased with 30% to 900 10^6 m^3. Due to several dams (Grevelingendam, closed in 1965; Volkerakdam, closed in 1969; Oesterdam, constructed between 1979-'86; and Philipsdam, constructed between 1977-'87), the mean freshwater load dropped from 70 to less than 20 m^3s^{-1} (Nienhuis & Smaal 1994b; Haas 1998).

The Oosterschelde is characterized by tidal channels, mudflats and large intertidal sandy shoals. Erosion of the intertidal area has been predicted to be an ongoing process with a reduction of 1.5 % per 5 years (van Berchum & Wattel 1997). The intertidal areas are important for the culture of cockles, while

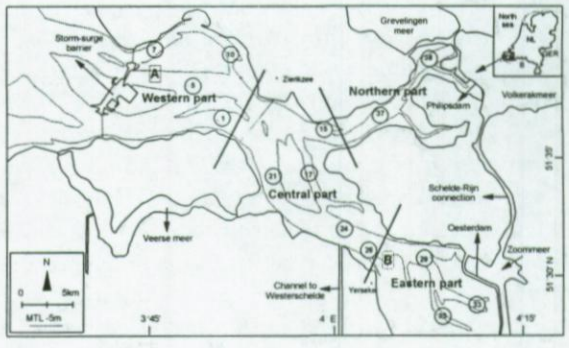

Fig. 4.1 Map of the Oosterschelde with 14 fish sampling locations (circles) in the subtidal area and 2 environmental sampling locations (A and B, from www.waterbase.nl). Note the division in a western, central, eastern and northern part

the shallow subtidal areas are important for the farming of oysters and mussels. There is high shipping and recreational activity in the subtidal area. The Oosterschelde can be divided into four geographical subareas: western (in the mouth), central, eastern (or basin) and northern part (see Fig. 4.1). The ecological and environmental properties of the Oosterschelde are explained in detail in Nienhuis & Smaal (1994a) and van Berchum & Wattel (1997).

4.2.2 Sampling

Juvenile fish and mobile macro-invertebrates have been investigated at the Centre for Estuarine and Marine Ecology (Yerseke, The Netherlands) at several locations during several periods. For the present study, data from 12 subtidal sampling locations (4 in the western, 5 central and 3 in the eastern part) were used from 10 quarterly surveys conducted between August 1987 and November 1989 (directly after the completion of the engineering works) and from 10 quarterly surveys conducted between August 1999 and November 2001 (a decade later) (Fig. 4.1, Table 4.1). Information is further given on the northern subarea, which was only investigated during the latter period (2 stations). Only the data for the fish fauna will be presented in this study, as during the first sampling period only a limited number of invertebrate species were taken into consideration. Primary data on all mobile macro-invertebrates from 1999-2001 will be presented elsewhere (Chapter 5).

Samples were taken with a three-metre beam trawl at an average depth of 13 metres below mean tidal level, operated from the RV Luctor (34 m, 500 Hp) and towed over a distance of 1000 metres at an average speed of 4.5 knots relative to the bottom. For most surveys the beam trawl was equipped with one tickler chain, a chain in the ground-rope and a fine-meshed net (5*5 millimetres in the cod end), except for November 1988 and February 1989 where a net of 10*10 millimetres was used.

To characterize the Oosterschelde environment in both periods averaged data on temperature (°C), salinity (psu), dissolved oxygen (mg.l^{-1}), suspended matter (mg.l^{-1}) and visibility (metres, measured as Secchi depth) were taken from the WaterBase website (Rijkswaterstaat NL, www.waterbase.nl). These were based on surface water analyses from two sampling locations in the western (Roggenplaat West) and eastern (Yerseke verwateringsplaats) subareas for the corresponding 20 months.

The fish species were counted, measured (as total length, TL in millimetres) and wet weighed. Densities were expressed as numbers per 1000 m², taking into account an overall 20% net-efficiency. Biomass was calculated by means of length-weight or number-weight regressions (Table 4.2), and was expressed in gram ashfree dry weight (ADW) per 1000 m². Three-dimensional plots show both temporal and spatial distribution patterns in density and biomass on a long-term scale for the commonest species that were identified during both periods. A Correspondence Analysis (CA) was performed on the averaged density data per station for both periods. A Canonical Correspondence Analysis (CCA) was performed on averaged density data per season for both periods, together with the associated environmental variables (also see §9.6.1). Prior to the multivariate analyses the data were fourth root transformed and reduced by eliminating those species with an average density (1987-2001) of less than 0.5 individuals per 1000m². Simple comparisons in number of species and frequency of occurrence between both periods were made. Mann-Whitney U tests were performed to identify significant differences in species diversity or in density and biomass per species between both periods. The seasonal, spatial and long-term differences in density and biomass for the separate species were presented per taxonomic group.

Table 4.1 Overview of the sampling surveys conducted in 1987-'89 (12 stations) and 1999-2001 (14 stations) in the Oosterschelde, with an indication of those stations where the sampling distance was reduced from 1000 to 500 metres or less to prevent clogging or tearing of the net

Season	Surveys during 1987-'89[1]		Surveys during 1999-2001	
	Date	Reduced	Date	Reduced distance
Winter	5, 8, 11 Feb 1988		7-8 Feb 2000	33, 35, 38
	14-15 Feb 1989		19-20 Feb 2001	33, 35, 38
Spring	13-14 Jul 1988[2]		15-16 May 2000	17, 24, 29, 33, 35, 38
	12-16 May 1989		21-22 May 2001	1, 5, 7, 33, 35, 38
Summer	17-18, 20 Aug 1987		30 Aug - 1 Sep 1999	29, 33, 35, 38
	23, 26 Sep 1988		28-29 Aug 2000	all (except 1 & 21)
	7-8 Aug 1989	29, 33	20-21 Aug 2001	26, 33, 35, 38
Autumn	6, 17-18 Nov 1987		22-24 Nov 1999	15, 35, 38
	14-17 Nov 1988		20-21 Nov 2000	33, 35, 38
	3-6 Nov 1989	1, 21	19–20 Nov 2001	26, 33, 35, 38

[1] No samples in the northern part (37 & 38); [2] Delayed due to bad weather conditions

Table 4.2 Species list, ecological guild, frequency of occurrence for 3 periods, range in total length and modal length class (between brackets for 1999-2001 if different from 1987-'89). Logarithmic length (mm) –weight (gram) regressions are given, as well as the slope of the allometric length conversions (in mm) in the formula TL = x SL for a few species. Ashfree dryweight (ADW) is on average 20% of wetweight (WW); TL = total length, SL = standard length

Order – Species	Guild[1]	% frequency of Occurrence[2]			Total length (mm)		Length-weight regressions (gram - mm)	Slope
		1960-'76	'87-'89	'99-2001	Range	Mode		
Clupeiformes								
Clupea harengus	MJ	19	28	24	50-310	95	lnWW= -13.19+3.233*lnTL (n=119, r^2=0.97)	
Sprattus sprattus	MJ	28	14	27	55-135	75 (65)	lnWW= -13.55+3.356*lnTL (n=141, r^2=0.99)	
Alosa fallax	CA	-	-	*	350		idem *Clupea harengus*	
Gadiformes								
Gadus morhua	MJ	8	18	4	50-590		lnWW= -12.326+3.139*lnTL (n=48, r^2=0.99)	
Merlangius merlangus	MJ	22	43	47	40-275	70 (60)	lnADW= -13.35+3.066*lnSL (n=47,r^2=0.98)	1.09
Trisopterus luscus	MJ	14	38	51	30-235	90 (130)	lnADW= -14.1+3.293*lnSL (n=45, r^2=0.97)	1.12
Ciliata mustela	MS	8	8	15	85-225	135 (160)	lnWW= -13.063+3.260*lnTL (n=33, r^2=0.98)	
Syngnathiformes								
Entelurus aeqoreus	MA	-	1	-	470		idem *Syngnathus acus*	
Syngnathus acus	ER	1	12	10	95-500	350 (225)	lnWW= -16.651+3.380*lnTL (n=75, r^2=0.99)	
Syngnathus rostellatus	ER	17	19	32	55-155	95	lnWW= -18.036+3.652*lnTL (n=38, r^2=0.98)	1.05
Scorpaeniformes								
Trigla lucerna	MJ	2	4	9	50-315	120 (160)	lnWW= -13.102+3.289*lnTL (n=38, r^2=0.99)	
Myoxocephalus scorpius	ER	33	48	24	65-295	150 (170)	lnWW= -11.983+3.148*lnTL (n=180, r^2=0.97)	
Enophrys bubalis	MA	1	°	9	45-115		idem *Myoxocephalus scorpius*	
Agonus cataphractus	ER	28	16	24	45-155	75	lnWW= -11.911+3.023*lnTL (n=153, r^2=0.99)	
Liparis liparis	ER	19	6	8	35-135	120 (60)	lnWW= -11.416+3.088*lnTL (n=53, r^2=0.99)	
Perciformes								
Gobius niger	ER	-	-	9	45-125		lnWW= -11.867+3.144*lnTL (n=32, r^2=0.98)	
Pomatoschistus microps	ER	12	4	30	20-50	30	lnWW= -11.404+2.931*lnTL (n=19, r^2=0.99)	
Pomatoschistus minutus	ER	74	67	92	20-90	65 (55)	lnWW= -13.440+3.404*lnTL (n=418, r^2=0.97)	1.16
Pomatoschistus lozanoi	MA	-	7	32	20-70	45	idem *Pomatoschistus minutus*	
Pomatoschistus pictus	MA	1	-	6	35-50		idem *Pomatoschistus minutus*	
Aphia minuta	ER	1	°	3	35-60		idem *Pomatoschistus minutus*	
Dicentrarchus labrax	MJ	2	7	21	50-315	100 (115)	lnWW= -11.749+3.061*lnTL (n=66, r^2=0.97)	
Trachurus trachurus	MA	6	5	5	30-105	80	lnWW= -11.443+2.955*lnTL (n=130, r^2=0.97)	
Chelon labrosus	MS	-	-	1	35		idem *Dicentrarchus labrax*	
Crenilabrus melops	ER	-	-	1	85-110		idem *Dicentrarchus labrax*	
Zoarces viviparus	ER	31	39	34	50-325	105	lnWW= -13.1+3.167*lnTL (n=165, r^2=0.96)	
Pholis gunnellus	ER	9	8	30	70-190	155	lnWW= -15.501+3.590*lnTL (n=31, r^2=0.98)	
Ammodytes tobianus	MA	16	10	21	80-200	155 (135)	lnADW= -16.737+3.551*lnTL (n=34, r^2=0.97)	1.09
Hyperoplus lanceolatus	MA	3	2	2	160-245		lnWW= -13.348+3.083*lnTL (n=22, r^2=0.99)	
Callionymus lyra	MA	14	33	55	50-245	85 (75)	lnWW= -10.465+2.724*lnTL (n=110, r^2=0.98)	
Pleuronectiformes								
Scophthalmus rhombus	MJ	4	2	3	170-340		lnWW= -12.374+3.212*lnTL (n=49, r^2=0.99)	
Lepidorhombus whiffiagonis	MA	-	-	1	145		idem *Limanda limanda*	
Pleuronectes platessa	MJ	82	91	86	20-415	90 (70)	lnWW= -11.690+3.033*lnTL (n=560, r^2=0.99)	1.22
Limanda limanda	MJ	59	78	74	35-280	60	lnWW= -12.330+3.161*lnTL (n=353, r^2=0.99)	1.23
Platichthys flesus	ER	43	24	34	60-400	185 (200)	lnWW= -11.051+2.926*lnTL (n=169, r^2=0.98)	
Microstomus kitt	MA	1	4	13	40-235	145 (170)	lnWW= -12.188+3.168*lnTL (n=22, r^2=0.99)	
Solea solea	MJ	48	30	36	55-410	90 (80)	lnWW= -13.097+3.262*lnTL (n=427, r^2=0.99)	1.13
Other species								
Anguilla anguilla	CA	22	11	5	100-700	500	lnWW= -15.245+3.326*lnTL (n=152, r^2=0.97)	
Osmerus eperlanus	CA	22	-	*	85-150		idem *Clupea harengus*	
Belone belone	MS	-	°	1	150		lnWW= -13.701+3.020*lnTL (n=9, r^2=0.99)	
Atherina presbyter	MJ	3	1	8	65-90		lnWW= -12.478+3.103*lnTL (n=12, r^2=0.99)	
Gasterosteus aculeatus	CA	7	5	-	30-55		lnWW= -11.359+2.938*lnTL (n=41, r^2=0.99)	
Species only recorded in 1960-76		1						
Lampetra fluviatilis, Raja clavata, Dasyatis pastinaca, Engraulis encrasicolus, Pollachius pollachius, Eutrigla gurnardus, Cyclopterus lumpus, Arnoglossus laterna, Scophthalmus maximus, Buglossidium luteum								
Number of species		44	32	38				

[1] estuarine resident (ER), marine juvenile (MJ), marine seasonal (MS), marine adventitious (MA), diadromous (CA)
[2] ° recorded in 1987-'89 but not in the stations considered in this study; * only caught in the northern part in 1999-2001

Table 4.3 Average density and biomass per species, total average, and number of species per season for 1987-'89 and 1999-2001 (between brackets). Significant differences (Mann-Whitney U-test) between both periods per season and in the overall comparison (middle column) are noted with * ($p<0.05$) and ** ($p<<0.001$)

Order/species	Density (#/1000m²)				Overall	Biomass (gADW/1000m²)			
	Winter	Spring	Summer	Autumn		Winter	Spring	Summer	Autumn
Clupeiformes									
Clupea harengus	9 (4) *	- (2)	1 (3)	12 (14)		30 (6) *	- (0.3)	1 (2)	15 (11)
Sprattus sprattus	6 (10)	- (0.4)	- (0.1)	11 (4)		4 (9)	- (0.5)	- (<0.1)	6 (2)
Gadiformes									
Gadus morhua	0.5 (0.2)	0.5 (-)	0.9 (0.6)	1 (-)		11 (18)	0.4 (-)	3 (2)	26 (-)
Merlangius merlangus	0.3 (0.5)	11 (7)	8 (8)	3 (4)		4 (6)	14 (13)	34 (36)	37 (65)
Trisopterus luscus	1 (3)	50 (8)	23 (50)	5 (5)		17 (43)	90 (1)	103 (256)	75 (67)
Ciliata mustela	- (0.3)	0.2 (0.2)	0.3 (0.5)	0.4 (0.8)		- (3)	2 (1)	<0.1 (1)	2 (4)
Syngnathiformes									
Entelurus aeqoreus	-	0.1 (-)	-	-		-	0.8 (-)	-	-
Syngnathus acus	-	0.3 (0.2)	1 (2)	0.2 (0.1)		-	2 (1)	2 (5)	0.6 (0.1)
Syngnathus rostellatus	0.1 (-)	0.2 (1)	3 (7)	1 (6)		<0.1 (-)	<0.1 (0.1)	0.2 (0.4)	0.1 (0.3)
Scorpaeniformes									
Trigla lucerna	-	0.2 (2) *	0.3 (0.1)	0.1 (-)		-	1 (16) *	3 (2)	0.1 (-)
Myoxocephalus scorpius	7 (1) *	4 (2)	5 (1) *	4 (1)	**	71 (34) *	45 (15)	65 (15) *	56 (20)
Enophrys bubalis	- (2)	-	- (1)	- (0.7)		- (3)	-	- (0.6)	- (1)
Agonus cataphractus	0.6 (0.6)	0.3 (1.1)	0.6 (2)	1 (3)		0.7 (0.3)	0.4 (1)	1 (1)	2 (4)
Liparis liparis	- (0.1)	- (0.4)	0.2 (1)	4 (0.2)		- (0.5)	- (0.1)	0.3 (1)	20 (1)
Perciformes									
Gobius niger	- (0.6)	- (0.2)	- (0.5)	- (0.5)		- (2)	- (0.5)	- (1)	- (1)
Pomatoschistus microps	0.2 (20) **	-	0.6 (3)	- (4.1) *	**	<0.1 (2) **	-	0 (0.2)	- (0.4) *
Pomatoschistus minutus	25 (351) **	4 (20) **	21 (304) **	85 (225) **	**	15 (139) **	2 (8) **	6 (68) **	38 (86) **
Pomatoschistus lozanoi	0.1 (1)	0.5 (2)	0.3 (3)	0.3 (2) *	**	<0.1 (0.2)	0.1 (0.3)	0 (0.2)	<0.1 (0.3) *
Pomatoschistus pictus	-	- (0.3)	-	- (13)		-	- (<0.1)	-	- (1)
Aphia minuta	- (0.1)	- (0.2)	-	- (0.1)		- (0)	- (0.1)	-	- (<0.1)
Dicentrarchus labrax	0.5 (10)	-	0.2 (0.1)	5 (14) *	*	1 (52)	-	0.1 (5)	9 (49) *
Trachurus trachurus	-	-	1 (1)	-		-	-	0.7 (1)	-
Chelon labrosus	-	-	-	- (<0.1)		-	-	-	- (<0.1)
Crenilabrus melops	- (0.2)	-	- (0)	- (0.2)		- (0.2)	-	-	- (0.4)
Zoarces viviparus	5 (1)	4 (3)	4 (13)	6 (2)		19 (4)	27 (9)	22 (39)	24 (7)
Pholis gunnellus	0.1 (2) *	0.5 (5) *	2 (4)	- (0.5)	**	0.2 (4) *	1 (10) *	4 (7)	- (0.4)
Ammodytes tobianus	0.1 (1) *	0.8 (-)	0.5 (4)	0.3 (0.7)		0.3 (1) *	4 (-)	2 (13)	1 (1)
Hyperoplus lanceolatus	-	-	0.1 (0.1)	0.1 (-)		-	-	0.6 (0.4)	0.1 (-)
Callionymus lyra	0.3 (2)	1 (10)	3 (32)	6 (29) **	**	0.3 (5)	3 (20)	7 (44)	13 (50) **
Pleuronectiformes									
Scophthalmus rhombus	- (0.1)	- (0.1)	- (0.1)	0.1 (0.1)		- (2)	- (1)	- (7)	4 (1)
Lepidorhombus whiffiagonis	-	-	- (0.1)	-		-	-	- (0.6)	-
Pleuronectes platessa	57 (29)	56 (74)	98 (233)	156 (33)	*	435 (112) *	749 (456)	1351 (1358)	1257 (194) *
Limanda limanda	69 (19)	12 (14)	17 (95)	138 (21)		212 (24)	39 (64)	32 (62)	245 (57) *
Platichthys flesus	2 (3)	2 (4)	1 (1)	1 (1)		46 (27)	28 (51)	19 (36)	42 (58)
Microstomus kitt	- (0.1)	0.4 (3)	0.1 (2)	- (0.7)		0 (1)	4 (23)	0.5 (12)	- (5)
Solea solea	12 (1)	4 (6)	5 (23) *	2 (1)		23 (2)	41 (49)	29 (144) *	8 (3)
Other species									
Anguilla anguilla	- (0.1)	1.5 (-)	1 (0.5)	0.1 (-)		- (5)	71 (-)	34 (22)	4 (-)
Belone belone	-	-	- (0.1)	-		-	-	- (<0.1)	<0.1 (-)
Atherina presbyter	-	-	- (0.1)	0.1 (0.7)		-	-	- (<0.1)	<0.1 (0.5)
Gasterosteus aculeatus	1.2 (-)	-	0.7 (-)	-		0.2 (-)	-	0.1 (-)	-
Total average	198 (463)	153 (165)	199 (794) *	444 (389) *	**	892 (506)	1124 (744)	1721 (2139)	1886 (691)
# species	20 (28) *	22 (25)	27 (33)	25 (29) *	**				

To investigate possible real long-term changes in the Oosterschelde (including the northern part), the number of species and the frequency of occurrence in 1999-2001 were compared with 1960-'76, where fish were investigated on basis of a similar sampling methodology (Doornbos *et al.* 1981).

Table 4.4 Average density and biomass per species, total average, and number of species per subarea for 1987-'89 and 1999-2001 (between brackets). Significant differences (Mann-Whitney U-test) between both periods are noted with * ($p<0.05$) and ** ($p<<0.001$)

Order/species	Density (#/1000m²)				Biomass (gADW/1000m²)			
	Western	Central	Eastern	Northern	Western	Central	Eastern	Northern
Clupeiformes								
Clupea harengus	3 (4)	5 (4)	11 (13)	(79)	5 (2)	4 (4)	30 (11)	(43)
Sprattus sprattus	2 (4)	1 (4)	13 (3)	(117)	2 (3)	1 (3)	6 (2)	(31)
Alosa fallax	-	-	-	(0.1)	-	-	-	(0.1)
Gadiformes								
Gadus morhua	2 (1)	0.4 (<0.1)	0.3 (-)	(0.1)	29 (12)	2 (<0.1)	2 (-)	(0.5)
Merlangius merlangus	12 (8)	3 (5) *	1 (0.5)	(5)	55 (69)	14 (23) *	4 (2)	(9)
Trisopterus luscus	21 (35)	13 (16)	24 (1)	(3)	131 (216)	21 (80)	90 (3)	(13)
Ciliata mustela	0.2 (1)	0.2 (0.5)	0.4 (-)	(-)	1 (3)	0.2 (3)	2 (-)	(-)
Syngnathiformes								
Entelurus aeqoreus	-	<0.1 (-)	-	(-)	-	0.4 (-)	-	(-)
Syngnathus acus	0.2 (0.1)	0.5 (1)	0.3 (1)	(0.5)	1 (0.1)	1 (3)	2 (1)	(0.4)
Syngnathus rostellatus	0.6 (3)	2 (4)	1 (6) *	(16)	<0.1 (0.2)	0.1 (0.2)	<0.1 (0.3) *	(1)
Scorpaeniformes								
Trigla lucerna	0.2 (1)	0.1 (0.5)	-	(0.1)	3 (5)	1 (6)	-	(1)
Myoxocephalus scorpius	4 (1)	7 (1) **	4 (1) *	(2)	55 (21)	71 (22) **	47 (17) *	(17)
Enophrys bubalis	-	- (1)	- (1)	(0.5)	-	- (1.2)	- (2)	(1)
Agonus cataphractus	1 (4)	0.7 (1)	0.1 (0.2)	(-)	2 (4)	1 (1)	0.1 (0.3)	(-)
Liparis liparis	3 (1)	0.3 (0.3)	0.2 (0.1)	(0.1)	16 (1)	1 (1)	1 (0.1)	(0.1)
Perciformes								
Gobius niger	-	- (0.2)	- (1)	(3)	-	- (0.9)	- (3)	(6)
Pomatoschistus microps	<0.1 (4)	- (3)	1 (16) **	(3)	<0.1 (0.4)	- (0.3)	<0.1 (2) **	(0.3)
Pomatoschistus minutus	17 (133) **	17 (235) **	100 (364) *	(1126)	8 (41) **	9 (76) **	41 (121) *	(301)
Pomatoschistus lozanoi	1 (4) *	- (2) *	2 (0.1)	(-)	0.1 (0.4) *	- (0.2) *	- (<0.1)	(-)
Pomatoschistus pictus	-	- (10)	- (0.2)	(1)	-	- (0.6)	- (<0.1)	(<0.1)
Aphia minuta	- (0.1)	- (0.1)	-	(-)	- (<0.1)	- (<0.1)	-	(-)
Dicentrarchus labrax	- (4)	0.3 (3)	6 (15)	(35)	- (23)	0.4 (19)	12 (47)	(123)
Trachurus trachurus	- (0.4)	1 (0.5)	0.1 (0.1)	(-)	- (0.3)	0.5 (0.4)	<0.1 (0.2)	(-)
Chelon labrosus	- (<0.1)	-	-	(-)	- (<0.1)	-	-	(-)
Crenilabrus melops	-	-	- (0.4)	(-)	-	-	- (0.7)	(-)
Zoarces viviparus	8 (8)	5 (6)	0.5 (0.4)	(27)	33 (23)	26 (20)	4 (0.3)	(61)
Pholis gunnellus	- (3) **	1 (3)	0.5 (2)	(10)	- (6) **	3 (5)	1 (3)	(12)
Ammodytes tobianus	1 (0.4)	0.2 (4) *	0.2 (0.1)	(-)	4 (1)	1 (11) *	1 (0.2)	(-)
Hyperoplus lanceolatus	<0.1 (<0.1)	0.1 (<0.1)	-	(-)	0.1 (0.2)	0.4 (0.1)	-	(-)
Callionymus lyra	5 (14) **	3 (36) **	1 (3)	(19)	10 (32) **	6 (49) **	2 (8)	(30)
Pleuronectiformes								
Scophthalmus rhombus	-	- (0.1)	0.1 (0.1)	(-)	-	- (6)	5 (1)	(-)
Lepidorhombus whiffiagonis	-	- (<0.1)	-	(-)	-	- (0.4)	-	(-)
Pleuronectes platessa	211 (230)	49 (52)	33 (9) **	(186)	2330 (1340)	353 (254)	382 (111) **	(297)
Limanda limanda	127 (84)	40 (31)	14 (3) **	(20)	240 (96)	90 (47)	62 (7) **	(23)
Platichthys flesus	2 (4)	0.4 (1)	2 (1)	(2)	47 (88)	8 (17)	55 (30)	(40)
Microstomus kitt	- (1)	0.3 (2)	-	(0.4)	- (9)	2 (17)	-	(0.2)
Solea solea	12 (20)	1 (4)	3 (1)	(17)	38 (86)	6 (60)	34 (4)	(48)
Other species								
Anguilla anguilla	1 (0.1)	0.2 (0.3)	1 (-)	(0.2)	40 (6)	8 (14)	36 (0)	(8)
Osmerus eperlanus	-	-	-	(1)	-	-	-	(2)
Belone belone	-	- (<0.1)	-	(-)	-	- (<0.1)	-	(-)
Atherina presbyter	<0.1 (0.1)	- (0.4)	- (0.2)	(0.1)	<0.1 (0.1)	- (0.3)	- (0.1)	(<0.1)
Gasterosteus aculeatus	0.6 (-)	0.5 (-)	0.2 (-)	(-)	0.1 (-)	0.1 (-)	<0.1 (-)	(-)
Total average	434 (570)	153 (432) **	221 (442)	(1671)	3050 (2089)	633 (745)	822 (376) **	(1066)
# species	25 (31) **	28 (36) **	27 (28)	(28)				

4.3 Results

4.3.1 Species richness and frequency of occurrence

A total of 42 fish species were caught in the Oosterschelde (Table 4.2). For the comparison between both periods all averages were calculated for 12 stations, excluding the northern part. In 1987-'89 an average of 21 species were noted in winter (February) and spring (May) and 26 species in summer (August) and autumn (November). In 1999-2001 5 fish species more were caught on average, which was significantly different for autumn and winter and in the overall comparison (Table 4.3). The number of species per station averaged around 20 in 1987-'89, while a significantly higher number was noted in the western and central parts in 1999-2001 (Table 4.4).

In the northern part 28 species were recorded during 1999-2001.

Only 3 species were recorded in more than 75% of all samples (Table 4.2). Most species were less common: 50-25% (9 species), 25-10% (10 species), 10-1% (13 species). The other 5 species were caught only once or occurred in less than 1% of the samples. More than 70% of the 40 species that were caught in the Oosterschelde excluding the northern part, showed an increased occurrence in 1999-2001 (>20% for 3 *Pomatoschistus* species, butterfish *Pholis gunnellus* and dragonet *Callionymus lyra*); 10 species were found in fewer samples during 1999-2001 (>20% difference for bull-rout *Myoxocephalus scorpius*).

4.3.2 Total average density and biomass

Sand goby *Pomatoschistus minutus* and plaice *Pleuronectes platessa* showed average densities of 135 and 100 ind/1000m² respectively, and only 3 species had average densities between 50-10 ind/1000m². More than 85% of the species were less abundant: 10-0.1/1000m² (15 species), 1-0.1/1000m² (14 species), and < 0.1/1000m² (6 species). 28 species showed an increased average density in 1999-2001 (largest difference for sand goby, but also significantly higher for dragonet, two other gobiid species and butterfish (Table 4.3). On the other hand, 9 species had decreased densities, with the largest (but not significant) difference for dab *Limanda limanda*. Only in terms of density, a significant increase was noted for summer and for the overall comparison between 1987-89 and 1999-2001, and a significant decrease for autumn. The total average density per season was 150 in spring, 200 in winter-summer, and 440 ind/1000m² in autumn in 1987-89, and 160 in spring, 390 in autumn, 460 in winter, and 790 ind/1000m² in summer in 1999-2001 (Table 4.3). The average density was significantly higher in the central part in 1999-2001 (Table 4.4). The average density varied between 150 (central), 220 (eastern) and 430 (western) ind/1000m² in 1987-89 and between 430 (central), 440 (eastern), 570 (western) and 1670 (northern) ind/1000m² in 1999-2001.

In terms of biomass, highest average values were found for plaice (800 gADW/1000m²). The further distribution in biomass classes was comparable with the density data: 100-50 gADW/1000m² (2 species), 50-10 gADW/1000m² (9 species), 10-1 gADW/1000m² (12 species), 1-0.1 gADW/1000m² (9 species), and <0.1 gADW/1000m² (7 species). In 1999-2001 26 species showed an increased biomass, which was significant for the same species as with the density data, supplemented with seabass *Dicentrarchus labrax*, but also a non-significant increase for bib *Trisopterus luscus*, whiting *Merlangius merlangus* and lemon sole *Microstomus kitt* was noted (Table 4.3). For the other 14 species, the average biomass decreased (significantly for plaice and bull-rout, and a large but not significant decrease for dab). The total average biomass varied per season between 890-1890 gADW/1000m² in 1987-'89 and between 510-2140 gADW/1000m² in 1999-2001. The total average biomass was significantly lower in the eastern part. Per subarea the values varied between 630 (central), 820 (eastern) and 3050 (western) gADW/1000m² in 1987-89 and between 380 (eastern), 750 (central), 2090 (western) and 1070 (northern) gADW/1000m² in 1999-2001.

4.3.3 Community analyses

Total inertia of the Correspondence Analysis based on the average density per station and per period of 23 species amounted to 0.29 (Fig. 4.3). The eigenvalues of the first two ordination axes were 0.08 and 0.05, respectively. The stations were found together more or less in a western, central and eastern group for both periods, corresponding with the geographical subareas. Canonical Correspondence Analysis clearly divided autumn and winter from spring and summer along the first ordination axis (Fig. 4.2). Winter was characterized by very high concentrations of suspended matter (15 $mg.l^{-1}$) as opposed to an average concentration of 5.5 $mg.l^{-1}$ for the other seasons, which was comparable for both periods (Table 4.5). Typical species for autumn were herring *Clupea harengus* and sprat *Sprattus sprattus* for both periods, and seabass and common goby *Pomatoschistus microps* for winter in the period 1999-2001. Spring and summer were characterized by higher temperatures (13.5 and 19 °C, respectively). Most species were found in these seasons. A further arrangement of seasons and periods could be seen along the second ordination axis. The period 1987-'89 was characterized by a higher visibility of the water, with high values for spring (up to 3.5 m) and summer (2.8 m). Typical species were cod *Gadus morhua*, whiting and bull-rout in 1987-'89, while sea-snail *Liparis liparis*, lozano's goby *Pomatoschistus lozanoi* and lemon sole were characteristic for 1999-2001. The total variance explained by the first two ordination axes amounted to 29 and 9 % respectively. Except for autumn, the first period showed somewhat higher dissolved oxygen concentrations, varying between 7

Table 4.5 Averaged environmental data per season for 1987-'89 and 1999-2001 (between brackets), recalculated from www.waterbase.nl (Rijkswaterstaat, the Netherlands)

Variable	Winter	Spring	Summer	Autumn
Salinity (psu)	30.3 (30.3)	30.2 (29.0)	30.8 (31.5)	31.1 (31)
Temperature (°C)	5.5 (5.5)	13.2 (14.0)	18.4 (20.1)	10.3 (8.9)
Secchi depth (m)	1.6 (1.0)	3.5 (1.8)	2.8 (2.1)	2.6 (1.9)
Dissolved oxygen ($mg.l^{-1}$)	10.6 (10.2)	10.4 (9.5)	8.3 (7.4)	8.7 (9.3)
Suspended matter ($mg.l^{-1}$)	15.3 (14.6)	6.3 (5.6)	5.1 (4.0)	5.9 (6.0)

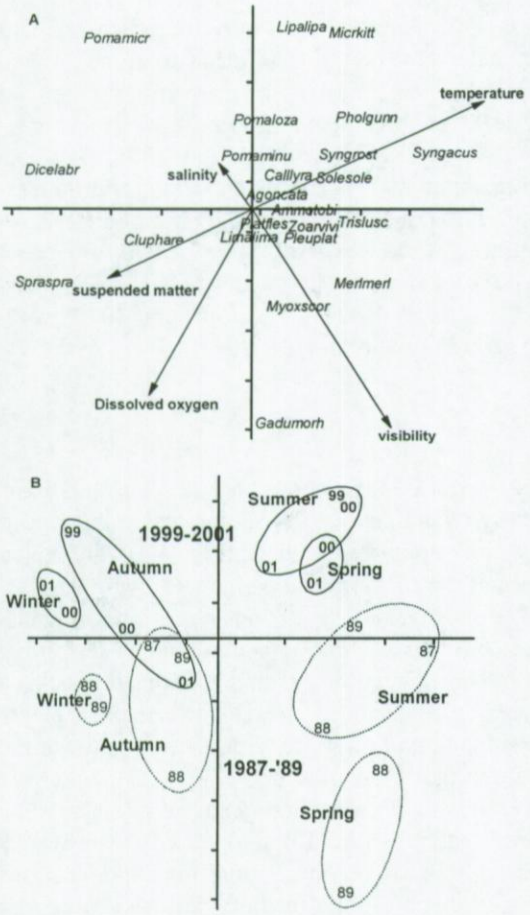

Fig. 4.2 Species (A) and sample-environmental (B) plots as a result of the Canonical Correspondence Analysis in the plane of the first two ordination axes. Surveys grouped per season and per period

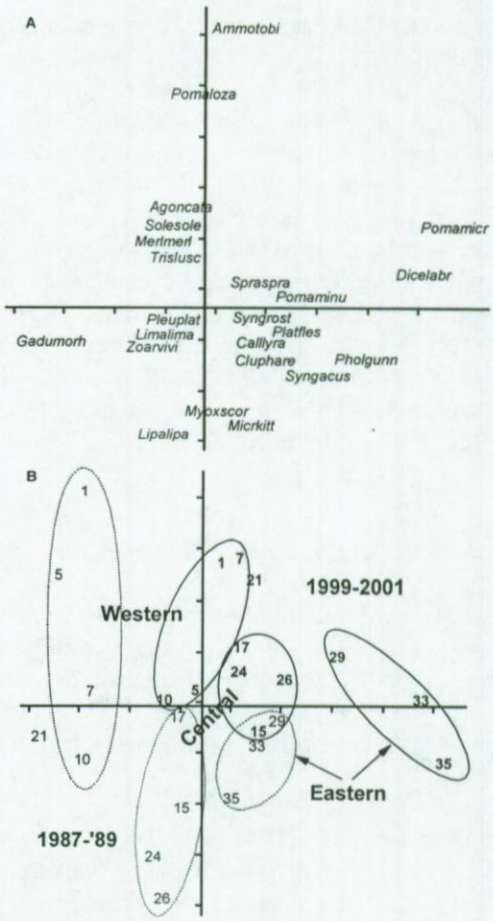

Fig. 4.3 Species (A) and sample (B) plots as a result of the Correspondence Analysis in the plane of the first two ordination axes. Stations grouped per subarea and per period

and 11 mg.l^{-1}. Salinity did not vary much between both (30.5 psu) (Table 4.5).

4.3.4 Comparison 1960-76 with 1999-2001

In 1960-76 a total of 44 fish species were recorded in the Oosterschelde (including the northern part), of which 12 and 11 species were not found in 1987-'89 and 1999-2001, respectively (Table 4.2). During the latter period 40 fish species were recorded, with 6 species that were not found in 1960-76. In both cases these were mainly species that were only recorded once. Three species were most common in both periods: sand goby, plaice and dab. Five species had an increased frequency of occurrence >20% (dragonet, bib, butterfish, whiting and seabass), 7 species between 20-10 %, 7 species between 10-5%, 3 species between 5-1%, and 6 species <1%. Three species had a decreased frequency of occurrence between 20-10% (smelt *Osmerus eperlanus*, eel *Anguilla anguilla* and sea-snail), 5 species between 10-5%, 4 species between 5-1%, and 10 species <1%.

4.3.5 Spatio-temporal patterns in density, biomass and growth

The average density and biomass per season and per station for both periods is given in Fig. 4.4. The spatio-temporal distribution patterns of the 4 commonest species were comparable in terms of biomass as the ones presented for density (Fig. 4.5). The length-frequency distributions per season for both periods for 12 common species were given in Fig. 4.6. The total length range and modal lengthclasses were given in Table 4.2. Average densities and biomasses per period, with a note on the significant differences for individual species, were given in Table 4.3 per season and in Table 4.4 per subarea.

Clupeiformes

Three clupeoid species were recorded in the Oosterschelde. Twaite shad *Alosa fallax* was caught only once at station 37 in November 1999. The two other species, herring *Clupea harengus* and sprat *Sprattus sprattus*, were mainly present in autumn and winter during both periods, and completely absent in spring and summer in 1987-'89.

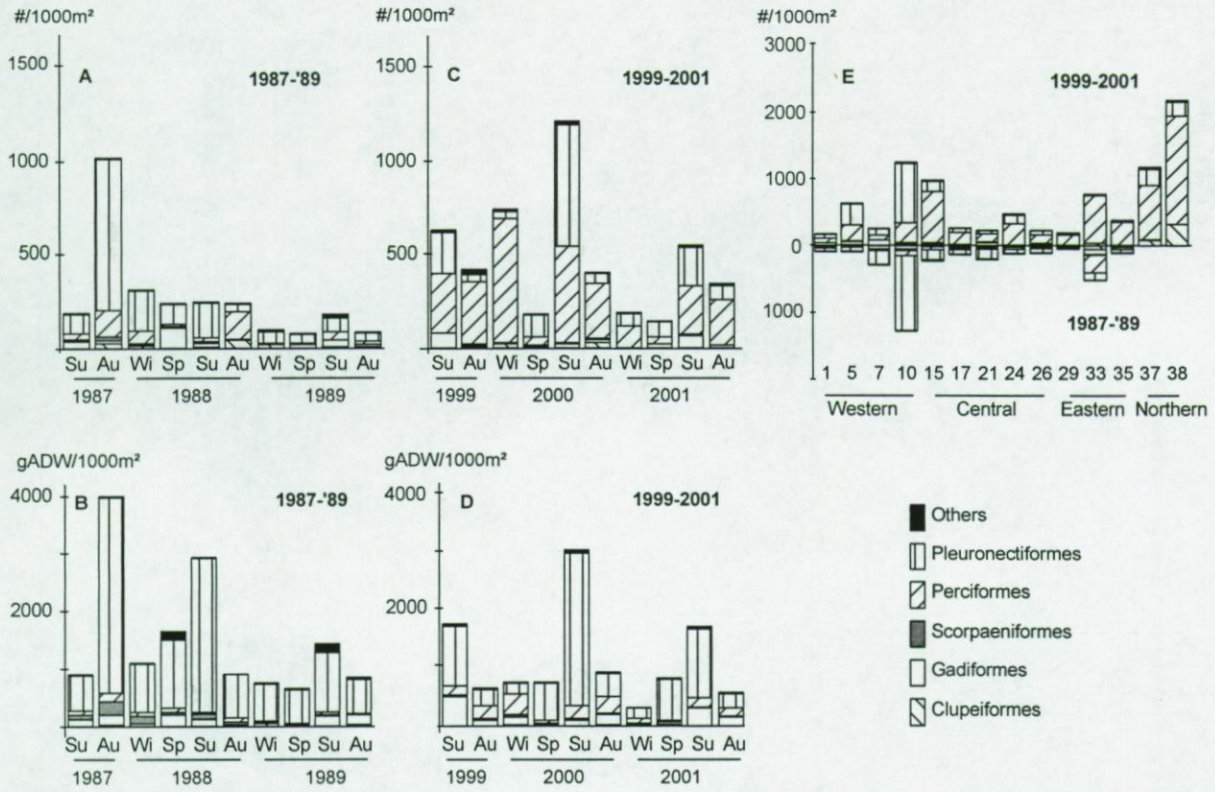

Fig. 4.4 Average density (A & C) and biomass (B & D) per seasonal survey (starting in summer 1987 and summer 1999, respectively), and average density per station (E) per taxonomic group for the periods 1987-'89 and 1999-2001

No significant differences were found for either species between both periods, nor per season or per station. Autumn was the richest season for *C. harengus* in both periods in numbers (on average 13 ind/1000m²); average biomass was highest in winter for 1987-'89 (30 gADW/1000m²) and in autumn for 1999-2001 (11 gADW/1000m²). This was mainly due to a number of large herring (>200 mm TL) that were caught during the first period, while in the latter period herring never exceeded a length of 150 mm. For *S. sprattus,* maximal density and biomass was recorded in autumn in 1987-'89 (11 ind/1000m² and 6 gADW/1000m²) and in winter in 1999-2001 (10 ind/1000m² and 9 gADW/1000m²).

Both species reached high densities in the eastern part (station 33) in 1987-'89, while this was only the case for herring in 1999-2001. Also, at station 15 high densities were recorded for herring in both periods, while this was only the case in 1999-2001 for sprat. For both species, highest average densities were recorded in the northern part during the latter period, with on average 120 and 200 ind/1000m² at station 38 for herring and sprat respectively. In this subarea herring and sprat were mainly present in summer and autumn.

Small juveniles (<60 mm) of *C. harengus* were only caught in spring. The bulk varied between 85 and 100 mm in length in autumn, while in February mainly larger individuals of 105-115 mm were present. For *S. sprattus* the modal length was 75 mm TL in 1987-'89, and a little bit smaller in 1999-2001 (65 mm). For both periods, the larger individuals (up to 130 mm) were only caught in winter.

Gadiformes

Four species were caught in the Oosterschelde. Poor cod *Trisopterus minutus* was recorded sporadically in 1987-'89 at other locations than the ones considered here. The most abundant species were bib *Trisopterus luscus* and whiting *Merlangius merlangus*, which mainly occurred in spring and summer. No significant differences were found between both periods for both species, but *T. luscus* was more abundant in spring of 1987-'89 (on average 50 ind/1000m², 90 gADW/1000m²), and in summer of 1999-2001 (on average 50 ind/1000m², 260 gADW/1000m²). The density and biomass for whiting were comparable per season between both periods, except in spring when highest densities were recorded (11 and 7 ind/1000m²) and in autumn when highest biomasses were found (40 and 65 gADW/1000m², respectively for both periods).

Both bib and whiting were found throughout the Oosterschelde, but whiting preferred the western part in both periods. Densities of bib were higher at most stations in 1999-2001, although this difference was only significant in terms of biomass for station 5 (40 gADW/1000m² in 1987-'89 against 260 gADW/1000m² in 1999-2001). In the eastern part *T. luscus* was more abundant in 1987-'89, which was

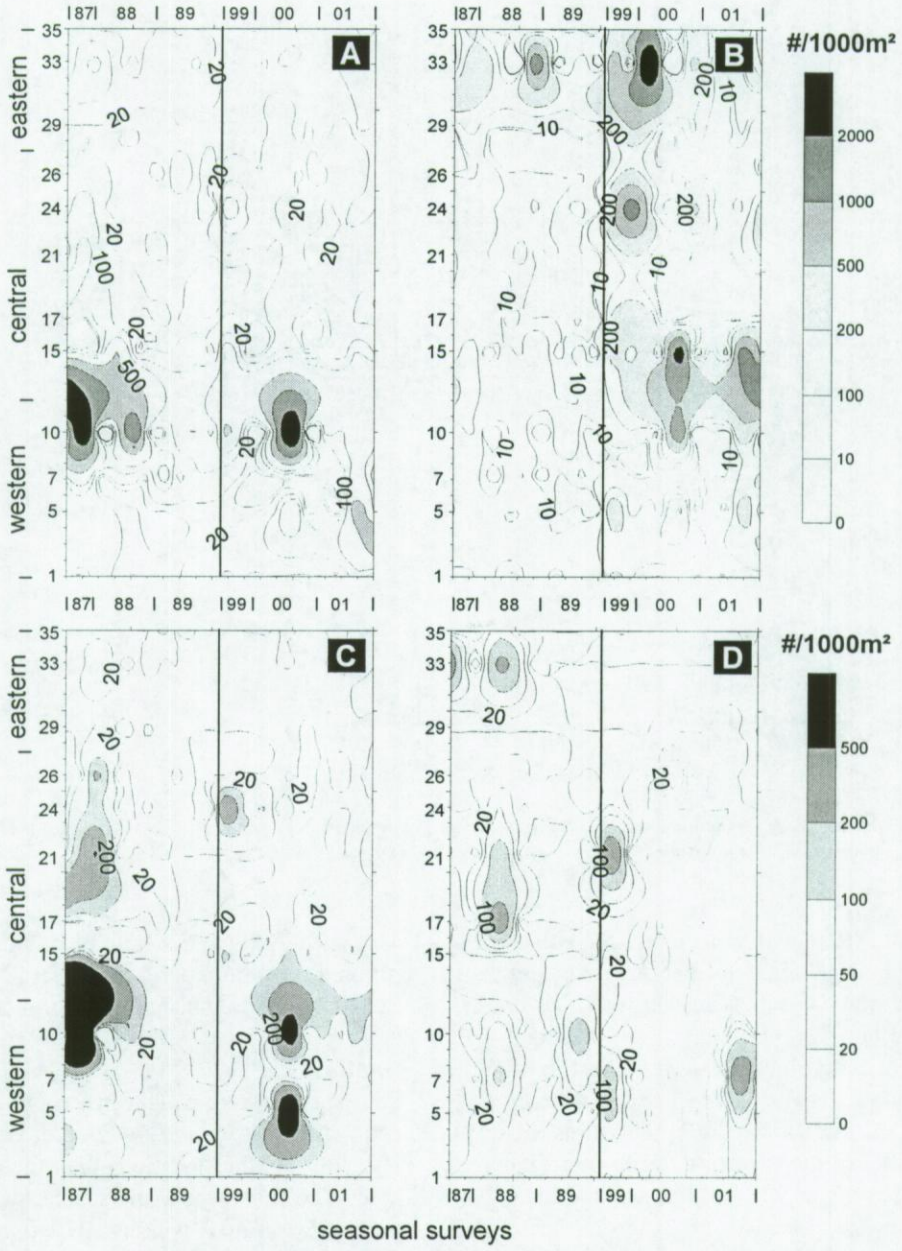

Fig. 4.5 Surface plots showing the spatio-temporal density patterns for *Pleuronectes platessa* (A) and *Pomatoschistus minutus* (B) (upper scale bar), and for *Limanda limanda* (C) and *Trisopterus luscus* (D) (lower scale bar). Seasonal surveys were successively ordered from August 1987 till November 1989 and from August 1999 till November 2001. Station numbers as in Fig. 4.1

mainly attributable to peak densities in summer 1987 and spring 1988. There was a clear growth observed from season to season for bib and whiting, with the smallest individuals found in spring (between 30-45 mm TL in 1999-2001 and 65-100 mm in 1987-'89 for bib, and between 40-90 mm TL for whiting). This was followed by the modal length classes 90 and 130 mm in both periods for bib and the length classes 115-165 mm for whiting in summer, and by a few larger individuals (up to 235 mm for bib and 275 mm for whiting) in autumn and winter.

Cod *Gadus morhua* and five-bearded rockling *Ciliata mustela* were much less common, and mainly elder individuals were caught. *C. mustela* was found in somewhat higher densities in 1999-2001 (0.5 ind/1000m²), and *G. morhua* was almost not found during this period (on average 0.8 and 0.2 ind/1000m² in 1987-'89 and 1999-2001 respectively). Both species were present at several stations in the Oosterschelde, but they were absent from the eastern part in 1999-2001. Bib, whiting and cod were also caught in the northern part at station 37, but never at station 38.

Syngnathiformes

Three pipefish species were recorded. Snake pipefish *Entelurus aequoreus* was only caught once in July 1988 at station 26. Nilsson's pipefish *Syngnathus rostellatus* was the most abundant species in the whole Oosterschelde, with a preference for the cen-

tral part (on average 4 and 12 ind/1000m² at station 15 in 1987-'89 and 1999-2001, respectively). The highest densities occurred in summer for both periods, and all length classes (55-155 mm TL) were present with a modal length class of 95 mm. In autumn of 1999-2001 *S. rostellatus* was also abundant in the length range 60-90 mm. The average density was twice as high in the latter period during summer and six times as high during spring and autumn, as compared to 1987-'89. *S. rostellatus* was also recorded in the northern part, with a peak abundance of 240 ind/1000m² in August 2000 in station 37.

Greater pipefish *Syngnathus acus* was not recorded in winter, and was present in most stations in low densities in spring and autumn (on average 0.2 ind/1000m²). The maximum average density in summer was twice as high in 1999-2001 (2 ind/1000m²). The length range of *S. acus* varied between 95 and 500 mm TL in 1987-'89 and between 125-405 mm in 1999-2001.

Scorpaeniformes

In this order 5 species were recorded. The most common species was bull-rout *Myoxocephalus scorpius*, followed by hooknose *Agonus cataphractus,* and sea-snail *Liparis liparis*, sea scorpion *Enophrys bubalis* and tub gurnard *Trigla lucerna.*

For *M. scorpius,* average densities were 3 to 5 times lower every season of 1999-2001, which was significantly different for winter (7 against 1 ind/1000m²) and summer (5 against 1 ind/1000m² in 1987-'89 and 1999-2001, respectively). In 1989 densities were much lower than in 1987 or 1988. The average biomass was 2 to 3 times higher in 1999-2001, with a maximum in winter (70 against 35 gADW/1000m²). Bull-rout was found throughout the Oosterschelde with higher densities at stations 10 and 26 in 1987-'89 and at stations 5 and 17 in 1999-2001 (significantly different in the central and eastern parts). Most length classes (65-295 mm TL) were present throughout the year, but three cohorts could be distinguished: a small cohort between 65 and 100 mm in winter (which was almost absent in 1999-2001), the commonest cohort between 100 and 175 mm, and elder species from 170 mm onwards.

A. cataphractus occurred at most stations with low densities, with a preference for the western part. During most seasons (except winter) this species was twice as abundant in 1987-'89. Higher average densities were recorded in autumn during all years (3 and 1.5 ind/1000m² in 1987-'89 and 1999-2001 respectively). Two successive cohorts could be seen, starting in summer with the commonest cohort between 45 and 95 mm TL, and a second year class between 90 and 155 mm.

L. liparis was found sporadically at several stations during 1999-2001. This species was almost absent in 1987-'89, except for a few records in autumn and summer, and an exceptionally high density in November 1987 at station 10 (120 ind/1000m²). In 1999-2001, the smallest individuals (35 mm TL) entered the Oosterschelde in February, and grew to a size of 135 mm in November. *E. bubalis* was only recorded in 1999-2001 (average density <1 ind/1000m²), although it was registered a few times in autumn and winter of 1987-'89 at locations not considered in this study. Sea scorpion did not occur in spring, nor in the western part. *T. lucerna* was only found in spring and summer, with significantly higher densities in May 2000 and 2001. Tub gurnard mainly occurred in the western part in 1987-'89, but also in the central part in 1999-2001. Length varied between 50 and 315 mm TL, with smallest and biggest individuals being recorded in summer, and the modal length classes in both periods (120, 160 mm) in spring. Most scorpaenid species, except hooknose, were also recorded in the northern part, but only *M. scorpius* was present in autumn throughout the whole period 1999-2001. *T. lucerna*, *L. liparis* and *E. bubalis* were recorded once in this subarea in spring, summer and autumn of 2001, respectively.

Perciformes

With 15 species, this order contained the highest number of fish species in the Oosterschelde. Sand goby *Pomatoschistus minutus* was the commonest species, followed by dragonet *Callionymus lyra*, viviparous blenny *Zoarces viviparus* and seabass *Dicentrarchus labrax*.

P. minutus occurred at all stations throughout the year, but density and biomass were significantly higher in 1999-2001 for all seasons and almost all stations (on average 40 and 230 ind/1000m² and 15 and 75 gADW/1000m² for 1987-'89 and 1999-2001 respectively). In both periods, density was lowest in spring and reached about the same value in the other seasons. Average density was highest in the eastern part at station 33 for both periods. This could mainly be attributed to very high densities in November 1988 (1600 ind/1000m²) and February 2000 (4700 ind/1000m²). This was also the main reason why the maximum average density and biomass had shifted from autumn in 1987-'89 to winter in 1999-2001. For the latter period, the average density was even higher in the northern part, with a peak density of 4140 ind/1000m² at station 38 in November 2001. In several other seasons the highest density was found at station 15 (on average 30 and 580 ind/1000m² in 1987-'89 and 1999-2001, respectively). The modal length classes (55, 65 mm TL) were present throughout the year. Still, growth could be seen through the seasons with the new recruits (20-40 mm) occurring in summer and autumn in the Oosterschelde, and larger individuals (up to 95 mm) found in autumn and winter of the succeeding year.

The four other gobiid species were much less common. In 1987-'89 common goby *Pomatoschistus microps* was only recorded in the eastern part in Feb-

ruary 1988 and in August 1989. The difference in density and biomass was significant for winter (on average 0.2 versus 20 ind/1000m²) and for autumn (0 versus 4 ind/1000m² in 1987-'89 and 1999-2001 respectively). In 1999-2001 *P. microps* was not found in spring, but during the other seasons it was found throughout the Oosterschelde, mainly in the eastern part (up to 20 ind/1000m² at station 33) and with a modal length of 30 mm TL. In the northern part average densities of 3 ind/1000m² were recorded. In 1987-'89 lozano's goby *Pomatoschistus lozanoi* was sporadically recorded in the western and eastern part and in 1999-2001 also in the central part. The length range varied between 20 and 70 mm. During all seasons density and biomass were higher in 1999-2001, although this was only significant for autumn and for station 7 (1 versus 6 ind/1000m²) and station 21 (0 versus 5 ind/1000m² for 1987-'89 and 1999-2001, respectively). Painted goby *Pomatoschistus pictus* was not recorded in 1987-'89. In February 2001 a few individuals were recorded. In November 2001 exceptionally high densities were found at station 15 (370 ind/1000m²) and at station 17 (100 ind/1000m²). In 1987-'89 black goby *Gobius niger* was caught at a station not considered in February 1989, while in 1999-2001 it was mainly found at station 35, with an average of 0.5 ind/1000m² for every season. Together with the previous species, *G. niger* was also found in the northern part, but never in the western part. Transparent goby *Aphia minuta* was sporadically recorded in 1999 and 2000, within a length range of 35-60 mm TL. It was caught a few times in July 1988 in the western part, but at stations not taken into consideration.

The density and biomass of *Callionymus lyra* were on average 5 to 10 times higher in 1999-2001, with a significant difference in autumn when the highest values were recorded (6 versus 29 ind/1000m² and 13 versus 50 gADW/1000m² in 1987-'89 and 1999-2001, respectively). Densities were lowest in winter. *C. lyra* preferred the western part, but in 1999-2001 also the central part with highest densities at station 15 (on average 110 ind/1000m²). Relatively high densities were recorded in summer and autumn in the northern part (on average 30 ind/1000m², 48 gADW/1000m² in 1999-2001). Two cohorts could be distinguished. The commonest year class entered the Oosterschelde in summer at 50 mm TL and grew till 130 mm in spring, followed by a second year class between 130 and 240 mm from summer onwards.

Zoarces viviparus was almost absent in 1989. Still, equal average densities and biomasses per season were recorded in both periods (5 ind/1000m², 21 gADW/1000m²). In 1999-2001, this species was mainly present in summer (on average 13 ind/1000m²), and this was the only season with higher densities than in 1987-'89. During both periods higher densities were recorded at station 10, and the species was sporadically caught in the eastern part. In 1999-2001 *Z. viviparus* was most abundant in the northern part (and at station 15), especially during spring and summer, with a maximum of 120 ind/1000m² at station 37 in summer 2000. At least two cohorts could be distinguished in both periods, with the smallest individuals (65 mm TL) of the commonest cohort starting in spring and growing till 145 mm in winter, followed by another cohort in spring which grew to 220 mm. Most probably the few bigger individuals belonged to other yearclasses.

Seabass *Dicentrarchus labrax* was not recorded in spring during both periods. For the period 1987-'89 it was found occasionally at stations 15 and 33 in summer 1987, winter 1988 and winter 1989, with an exceptionally high density at station 33 in November 1987 (170 ind/1000m²). In 1999-2001 *D. labrax* was a little bit more common at several stations in autumn (significantly different from 1987-'89) and winter (on average 14 and 10 ind/1000m² with 50 gADW/1000m² in both seasons). In comparison, high densities were recorded at station 37, but only in autumn 1999 and 2000 (130 and 530 ind/1000m²). In 1999-2001 the modal length class was 115 mm (100 mm in 1987-'89), and only a few larger individuals (up to 315 mm) were recorded.

Butterfish *Pholis gunnellus* was mainly found in the central and eastern parts at low densities in spring and summer in 1987-'89 (on average 1 ind/1000m²). In 1999-2001 *P. gunnellus* was more common throughout the Oosterschelde, also in the northern part (on average 10 ind/1000m²). The average density was significantly higher in spring and winter in 1991-2001 (resp. 5 and 2 ind/1000m²) and in the western part at station 5. The length range varied between 70 and 190 mm TL, with the smallest individuals occurring in summer.

Also sandeel *Ammodytes tobianus* was a little bit more common in 1999-2001 (on average 0.5 versus 2 ind/1000m² in 1987-'89 and 1999-2001 respectively), but the difference was only significant for winter and at station 21 in the central part. The highest average density and biomass was found in summer (5 ind/1000m², 13 gADW/1000m²), with a clear preference for station 17. *A. tobianus* was not found in the northern part. The modal length varied between 155 and 135 mm TL.

The other percid species were only sporadically recorded, and were not found in the northern part. The greater sandeel *Hyperoplus lanceolatus* was caught a few times in autumn 1987, summer 1988 and summer 1999. Scad *Trachurus trachurus* was found every year at several stations in summer with comparable densities and biomasses in both periods (on average 1 ind/1000m² and 1 gADW/1000m²), and within a length range of 30-105 mm TL. Thicklipped mullet *Chelon labrosus* was caught once at station 1 in November 2001. Corkwing wrasse *Crenilabrus melops* was recorded a few times in the

beam trawl samples from the eastern part in February 2000 and November 2001.

Pleuronectiformes

Seven flatfish species were recorded in the Oosterschelde. Megrim *Lepidorhombus whiffiagonis* was only caught once at station 15 in August 1999. The most common species were plaice *Pleuronectes platessa* and dab *Limanda limanda*. For both species average density and biomass were much higher in 1987-'89 during autumn and winter, although this was only significant in terms of biomass (on average 1260 versus 190 and 440 versus 110 gADW/1000m² for plaice, 250 versus 60 and 210 versus 25 gADW/1000m² for dab). On the other hand, densities were much higher in 1999-2001 during summer and comparable (per species) between both periods in spring. Both plaice and dab were present throughout the Oosterschelde, but in most cases highest densities were recorded at station 10 (on average 670 versus 680 ind/1000m² for plaice, and 440 versus 160 ind/1000m² for dab in 1987-'89 and 1999-2001, respectively). Significantly higher density and biomass were recorded at station 7 in 1987-'89 for plaice and at station 5 in 1999-2001 for dab, although this was not clear from the averages per subarea. For both species densities became significantly lower in the eastern part in 1999-2001, where they almost disappeared (a decrease from 70 to 2 ind/1000m² for plaice, and from 20 to 2 ind/1000m² for dab at station 33). In the northern part high densities were recorded for plaice (on average 190 ind/1000m²) and to a lesser extent for dab (on average 20 ind/1000m²) during the latter period.

All length classes of *P. platessa* were present throughout the year in both periods, except the smallest individuals (20-50 mm TL). These were only found in 1999-2001 in spring, and were followed by the commonest length classes (60-80 mm) in summer. In 1987-'89 the bigger modal length class (90 mm) was found in autumn. In February of both years a second cohort started with a length varying between 55 and 135 mm. This second year class was also more common in summer of 1999-2001 and in autumn of 1987-'89. By next winter the biggest individuals of this cohort had reached a length of 230 mm. Bigger and elder individuals (up to 415 mm) were only sporadically caught in both periods. The sex ratio for plaice was approximately 65% males and 35% females for all length classes, while for dab the sex ratio was 1:1. *L. limanda* entered the Oosterschelde in summer at a length of 35 mm TL in both periods. In 1999-2001 the commonest length ranged from 50 to 75 mm in summer, while in 1987-'89 the commonest length classes were found in autumn (50-100 mm). As with plaice, relatively high densities of small dab (40-90 mm) were recorded in winter of both periods. By the following summer the bigger individuals of this cohort had reached a length of 120 mm. The second cohort and elder individuals (up to 280 mm) were only sporadically caught in the Oosterschelde.

For sole *Solea solea* highest average densities were recorded in winter in 1987-'89. This could mainly be attributed to higher densities in February 1988 (25 ind/1000m²). Significantly higher densities and biomasses were found in summer in 1999-2001 (5 versus 25 ind/1000m² and 30 versus 145 gADW/1000m² in 1987-'89 and 1999-2001, respectively). *S. solea* preferred the western part in both periods, but high densities were also recorded in the northern part in 1999-2001 (on average 17 ind/1000m²). The new recruits (55 mm TL) entered the Oosterschelde in summer in both periods, and by next summer they had reached a length of 150 mm. For 1999-2001 a clear succession could be seen, while for 1987-'89 the commonest length classes were found in winter. Bigger and elder individuals (up to 410 mm) were sporadically caught in spring and summer of both periods.

The other 3 flatfish species were less common. The average density of flounder *Platichthys flesus* was a little higher for all seasons in 1999-2001 (on average 1.5 versus 2 ind/1000m² and 35 versus 45 gADW/1000m² in 1987-'89 and 1999-2001, respectively). The average density and biomass were a little higher in winter and spring for both periods. They were caught at several stations, but more in the western and eastern parts. Significant differences were found for station 10 (higher in 1999-2001) and for station 33 (lower in 1999-2001). *P. flesus* was also recorded in the northern part (on average 2 ind/1000m² in 1999-2001). The length varied from 60 to 400 mm TL, with the smallest individuals occurring in winter and a clear increase towards autumn and the following winter in both periods.

Lemon sole *Microstomus kitt* was caught a few times in the central part in July 1988 and August 1989. In 1999-2001 it mainly occurred in spring and summer with on average 2 ind/1000m², which was 10 times higher than in 1987-'89. In 1999-2001 *M. kitt* was mainly found in the central part, although a significant difference was noted for station 5. The species was never caught in the eastern part, and only occurred at station 37 in May 2000. Three distinct cohorts could be seen in 1999-2001, all starting in spring and ending in autumn with lengths between 40-110 mm, 120-190 mm, and 190-235 mm.

Brill *Scophthalmus rhombus* was caught a few times in autumn at stations 29 and 35 in 1987-'89, and a few times more in different seasons (on average 0.1 ind/1000m² every season) at stations 29 and 21 in 1999-2001. Mainly elder individuals were caught, with lengths varying between 170 and 340 mm TL.

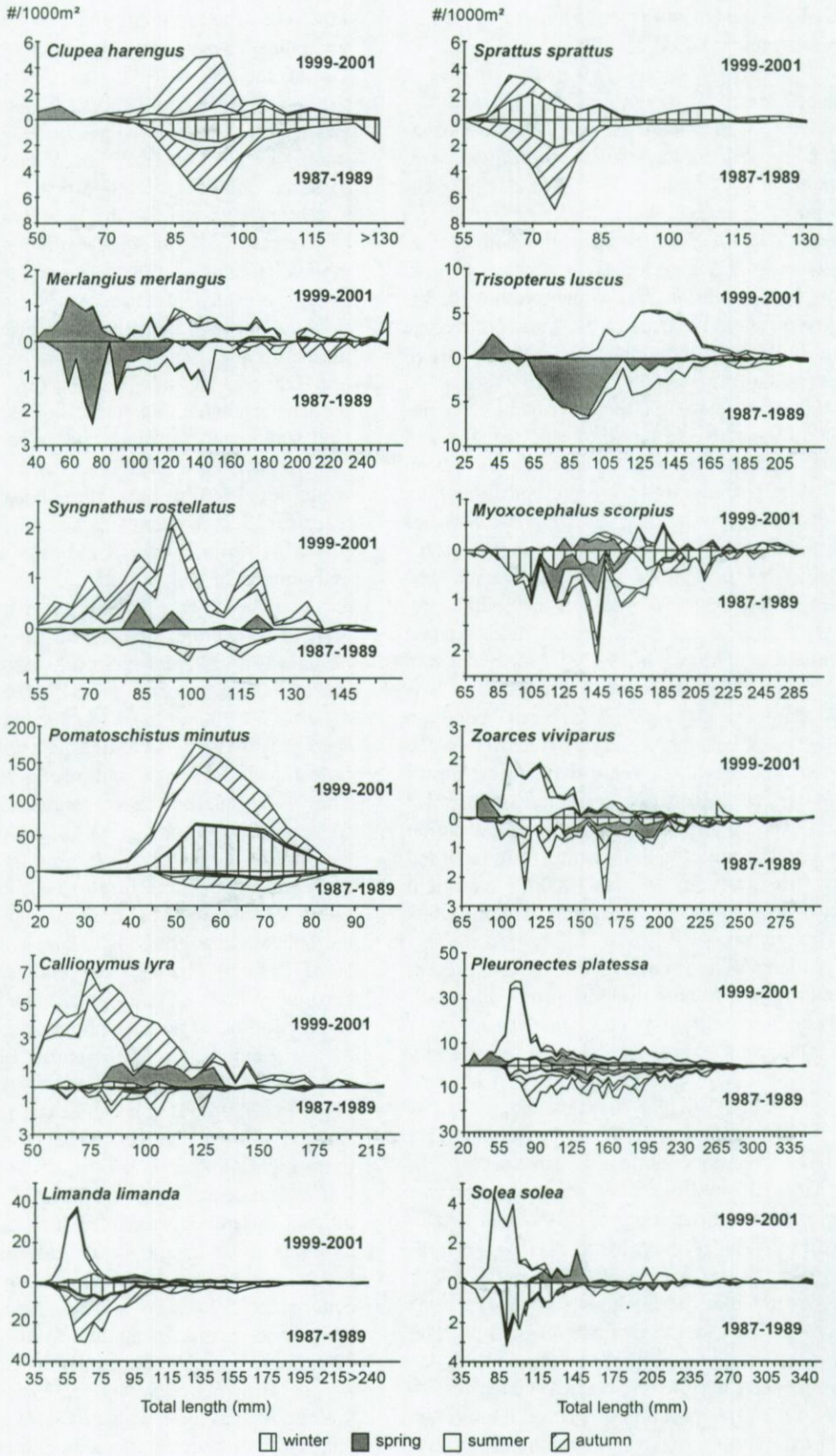

Fig. 4.6 Length-frequency distributions for 12 relevant species divided per season and compared between the two periods (1987-'89 and 1999-2001). Note the different scale bars

Other fish species

Six more species belonging to different taxonomic entities were occasionally recorded in the Oosterschelde. The average density and biomass of eel *Anguilla anguilla* was a little higher in 1987-'89 (0.7 ind/1000m² and 25 gADW/1000m² versus 0.2

ind/1000m² and 8 gADW/1000m²). In 1987-'89 it was caught mainly in spring and summer and in 1999-2001 mainly in summer, both at several stations. The length range varied between 100 and 700 mm TL, with the smallest individuals occurring in spring and mostly individuals >300 mm caught. *A. anguilla* was caught once at station 37 in August 2001.

Smelt *Osmerus eperlanus* was caught three times in the northern part in May 2000 and 2001 and in August 2001. Garfish *Belone belone*, although recorded once in July 1988 at a station not considered here, was caught once at station 21 (150 mm TL) in August 1999.

Sand-smelt *Atherina presbyter* was recorded once at station 7 in November 1989 and a few times at several stations in autumn and summer of 1999-2001. The length varied between 65 and 90 mm TL. *A. presbyter* was also found at station 37 in November 1999. Three-spined stickleback *Gasterosteus aculeatus* was caught a few times at several stations in winter and summer of 1987-'89 (on average 1 ind/1000m²). It was never recorded in 1999-2001. The length varied between 30 and 55 mm TL.

4.4 Discussion

4.4.1 Long-term overall differences

It seems difficult to find correlations between large-scale artificial changes to an ecosystem and changes in fish parameters. For example, no immediate changes in the fish fauna could be attributed to the building of the storm-surge barrier in the mouth of the Oosterschelde (Chapter 3; Chapter 3-Add.). Fish species are not only dependent on the Oosterschelde, but are influenced by recruitment to the adult North Sea stocks, yearclass strength, commercial fisheries (and bycatch), spawning possibilities, and larval movement. For example, in the Tagus estuary (Portugal) it was difficult to assess the relative importance of anthropogenic versus naturally induced fluctuations, due to the masking effect of a range of natural short-term variations (Cabral *et al.* 2001). The Oosterschelde is still changing: during the nineties the mussel farming practices have changed which resulted in an increased harvest (Smaal & Lucas 2000), commercial fisheries other than shellfisheries were banned due to the status of nature reserve (Wolff 1997), total cargo capacity and recreational activities have increased (van Berchum & Wattel 1997), and the option to partly restore the estuarine character of the Oosterschelde has been taken under consideration (Haas 1998). It is quite difficult to judge the influence of all these changes upon the fish fauna.

Inherent to the large spatial and temporal variability in fish populations within an estuary, is the ability of both the population and the environment to absorb and adjust to changes, where the population size can be regulated according to the available resources and the environment still can function normally. This was termed 'population and environmental homeostasis' (Elliott 2002). For example, by means of a partial Principal Component Analysis (with elimination of the temperature effect), it was shown that changes in the fish communities of the Oosterschelde in 1989 retrospectively evolved towards a state more or less comparable with the period 1983-'85 (Hostens *et al.* 1993).

In this study we investigated whether important changes had occurred in the fish fauna of the Oosterschelde, or if there was a kind of 'population homeostasis' over a ten years period after the major engineering works were completed. For this comparison, a reduction of the existing data had to be made (from 36 stations sampled between 1983-'89 to 12 stations between 1987-'89). The inevitable consequence was that a number of (mainly rare) species caught in 1987-'89 were lacking in the data set used, *e.g* pollack *Pollachius pollachius* (Feb. 1987), tadpole fish *Raniceps raninus* (May 1989) and lumpsucker *Cyclopterus lumpus* (Nov. 1988). In the last decades, a total of 73 fish species have been caught in the Oosterschelde with several sampling devices (Elliott & Hemingway 2002). Maandag (1999) calculated that an average reduction of 4 species could be expected if 12 instead of 36 stations were taken into account. However, species richness was between 15 and 20% higher in 1999-2001. Actually, four species (except painted goby) that were only present in 1999-2001 were also recorded in 1987-'89 at stations not considered in the present study (garfish, sea scorpion, transparent goby and black goby). Most species that were only caught once or a few times in any period have a real pelagic life style, *e.g* wrasses, mullets, scads, garfish, smelts and sand-smelts (Froese & Pauly 2002).

In comparison with 1960-'76 (Doornbos *et al.* 1981) 12 species occurred in fewer samples in 1999-2001. A number of the 'decreasing' species on this longer time scale (*e.g* hooknose and brill) were also found to have a decreased frequency of occurrence based on fyke catches between 1979 and 1988 (Chapter 3-Add.). On the other hand, several species that showed a decrease in the period 1979-'88 (*e.g* sand goby and five-bearded rockling) seemed to have increased when a comparison is made between 1960-'76 and 1999-2001. In total 23 species, amongst which abundant species like plaice, dab and sand goby, showed an increased frequency of occurrence from 1960-'76 as compared to 1999-2001. Frequency of occurrence is not the best indicator of change (Chapter 3-Add.), but at this time it was the only useful measurement. No comparison could be made in

terms of density since the 1960-'76 sampling was not always done during the same season or month, and only averaged data were given per 100 minutes sampling, which by conversion to a surface unit (1000m²) gave doubtful densities an order of magnitude lower than in 1999-2001. This could be related to the fact that for 1960-'76 the averages were calculated over a total of 356 samples from 43 surveys, while the averages for 1999-2001 were only based on 140 samples from 10 surveys. Nevertheless, two or three decades later the number of species caught with a beam trawl was still comparable.

On a shorter time scale (from 1987-'89 towards 1999-2001), 28 of the 40 species showed an increased frequency of occurrence after the engineering works were completed, and the most abundant species were abundant in both periods. Sand goby and dragonet were mainly responsible for the increase in total average densities with 45% from 260 to 480 ind/1000m². Without sand goby, the total average densities were comparable between both periods. The average biomass of all fish species together decreased with 35% from 1500 gADW/1000m² in 1987-'89 to 1100 gADW/1000m² in 1999-2001. This was mainly due to a reduced average weight of 2 flatfish species, namely plaice and dab, which was not reflected in terms of density. If those two species were excluded, the average biomass increased in the central and western part, and only decreased in the eastern part.

4.4.2 Long-term seasonal differences

On a temporal scale higher average densities were recorded for 3 seasons in 1999-2001, except in autumn. This was reflected in the Canonical Correspondence Analysis, where all seasons were separated per period while the autumn surveys overlapped each other. In winter and spring twice as many species showed an increased average density and biomass in the period 1999-2001. On average 23 species increased and 10 species decreased. In summer even 26 against 7 species increased. The difference was significant for 13 species within several seasons, but mainly in autumn (5 species increased, 2 species decreased significantly) and in winter (4 increased and 4 decreased). If data from the same periods and seasons were compared from the neighbouring Westerschelde estuary, most fish species showed a decreasing density (Chapter 9). Comparably, in the Tagus estuary (Portugal) a decreased abundance of many juvenile fish species (*e.g* bib, rockling, and flounder) was noted from 1978-'80 towards 1994-'96, which was mainly attributed to pollution, fishery regulation and waterflow control (Costa & Cabral 1999).

Six species showed an increased density and biomass throughout the whole period in all seasons. Lemon sole was only caught in 1999-2001, which was reflected in the Canonical Correspondence Analysis. According to the results of the Demersal Young Fish Surveys, the Oosterschelde was the only ecosystem along the Dutch coast where the O-group of this species was caught (Welleman *et al.* 2000). The large discrepancy between both periods for sand goby (on average 40 ind/1000m² for 1987-'89 and 230 ind/1000m² for 1999-2001) - as well as for the other *Pomatoschistus* species - could not easily be explained. The low density in 1987-'89 could be partly due to a reduced net efficiency for these small species as a bigger mesh size was used in November 1988 and February 1989. However, this does not explain why the density was equally low for example in November 1987 or 1989. On the other hand, data from a fortnightly study between 1987-'89 at 4 sampling points in the western and central Oosterschelde (Hostens & Hamerlynck 1993), showed that the average density for sand goby in summer and autumn (resp. 230 and 170 ind/1000m²) was in the same order of magnitude as was found for 1999-2001 in the present study. Most probably the low densities in 1987-'89 that were recorded in the present study were not really representative due to an unknown sampling error for these small gobiid species.

Respectively 13 and 14 species showed an increased density or biomass in 3 seasons. In some cases this was related to logistical sampling limits. The discrepancy in density and biomass for bib in spring was mainly due to the fact that in 1988 the spring survey was conducted in July, while all others were taken in May. Bib is a species with a typical seasonal occurrence, with the new recruits only starting to immigrate in May, while in July most juveniles already had arrived in the Oosterschelde. This resulted in a 'misleading' higher average density in spring of 1987-'89. For all other seasons the average density was higher in 1999-2001. On the other hand the appearance of the species themselves can be delayed. For example, herring and sprat reached highest average densities in autumn in both periods, except for 1999 and 1988 when the maximum density for sprat (respectively herring) was shifted from autumn to winter. This mainly explained why in the CCA most autumn surveys, except that of 1999 and 1988, were found close to each other. In the Thames estuary (UK) peak abundances of herring and sprat were found in December-March, which was correlated with high dissolved oxygen concentrations and low temperatures (Power *et al.* 2000a). Common goby and seabass were characteristic for winter in 1999-2001 in the ordination plot of the CCA. Both species showed a significant increase in the latter period in autumn and winter. Together with a few others (*e.g* bib), these were the only species that showed an increased density in 1999-2001 in the Westerschelde as well (Chapter 9).

For 9 species a decrease in density and biomass was noted in 2 seasons, *e.g* in autumn and winter for sole, plaice and dab. In contrast with the den-

sity values, the total average biomass decreased for every season in 1999-2001, except for summer. This could mainly be attributed to a similar discrepancy between both periods as was shown above, due to a delayed appearance of plaice and dab. The higher average densities in autumn and winter for the period 1987-'89 were mainly due to the fact that in 1987 the mass immigration of juvenile flatfish only started in autumn (which was still visible in winter 1988), while for the other years in both periods the highest densities of plaice and dab were always recorded in summer. No differences could be detected if only the total average density per period were compared (on average 100 ind/1000m² for plaice and 50 ind/1000m² for dab in both periods). The yearclass of 1987 appeared to be very strong, with high densities of plaice and dab present in the Oosterschelde. In the western Wadden Sea strong year classes for plaice were characterized by a delayed larval immigration of about 1 month, as eggs were only hatched in February-March after a cold winter (van der Veer *et al.* 2000). Moreover, within both periods the average densities of plaice and dab decreased from 1987 towards 1989 and from 2000 towards 2001. Also in the Thames estuary (UK) a successive decrease was recorded from 1987 towards 1989 for plaice, sand goby and flounder (Araujo *et al.* 2000).

Six species showed a decreased density in 3 seasons (*e.g* eel and viviparous blenny). Only cod and bull-rout decreased throughout the whole period 1999-2001. The probability to meet a bull-rout as a diver was calculated to be around 25% between 1997 and 2001, mainly in the central part of the Oosterschelde (A. Gmelig, www.anemoon.org). In a previous study based on data from 1983 till 1989, bull-rout was characteristic for the transitional period 1986-'87 (upon completion of the storm surge barrier in the mouth of the Oosterschelde), but declined towards 1989 (Hostens *et al.* 1993). A similar decreasing trend was seen in the German coastal zone of the North Sea (Tiews 1990). Perhaps, the cold winters of 1985-'87 were favourable to produce higher densities of bull-rout during that period, and in 1999-2001 (without preceding cold winters in the nineties, www.waterbase.nl) a population homeostasis similar to other periods and places was noted.

The length-frequency distributions showed that most seasons in both periods were characterized by juveniles, mainly O-group and to a lesser extent 1-group for a number of species. Based on the ecological guild concept (Elliott & Dewailly 1995), 13 species could be classified as estuarine resident and 11 species as marine juveniles, while 4 species were classified as catadromous and 14 species as marine seasonal or adventitious species. This proved the importance of the Oosterschelde both as a nursery and feeding area. More than half of the species reached their highest abundance in summer or autumn (respectively 7 and 14 species in 1987-'89, 17 and 7 species in 1999-2001), which was also clear from the Canonical Correspondence Analysis. Similar results were recorded within the Demersal Young Fish Surveys, with an overall dominance of O-group (and 1-group) and the most abundant species in fall being plaice, dab, sole and herring between 1970-1999 (Welleman *et al.* 2000). For several species the bigger individuals emigrated in winter or showed a growth stop from autumn to winter. For plaice and dab this resulted in a 'negative' growth. According to Welleman *et al.* (2000) the modal length was 90 mm TL in September and 100 mm in March for plaice, and 50 and 60 mm respectively for dab. In the present study the modal length classes for plaice were 75 mm TL in autumn and 90 mm in winter for 1999-2001, and 90 respectively 80 mm for 1987-'89 in autumn and winter. For dab the modal length classes in both periods were 60-65 and 70-75 mm in autumn, which closer resembled the results of Wheeler (1969).

4.4.3 Long-term spatial differences

From the Correspondence Analysis it was clear that the stations were arranged together more or less in geographical entities per period, and that the similarity between both periods per subarea was larger than the difference between the subareas. In a previous study based on data from 1988-'89, the western part was divided in two subareas (Chapter 3), but for 1999-2001 this distinction was not appropriate anymore. Apparently, some spatial differences were noted between both periods in terms of density and biomass. Six species showed an increased abundance in at least 10 stations (excluding the northern part), while another 9 species increased in more than half of the stations. The main species that increased in almost the whole Oosterschelde in 1999-2001 were 3 *Pomatoschistus* species, seabass, nilsson's pipefish and dragonet. In a comparative study with neighbouring areas, the latter species was found to be an indicator species for the Oosterschelde (Chapter 3). On the other hand, 4 species had decreased in >50% of the stations, with lower average densities for bull-rout recorded at 10 stations in 1999-2001. For 11 species the difference was significant in at least one subarea, with a significant difference for 6 species at station 5, and between 2 and 4 species at the other stations, except for station 1.

In the western part 8 species showed a decreased density and 20 species increased. The decrease in whiting densities in the western part in 1999-2001 was of minor importance, as the average density was in the same order of magnitude per station. In terms of biomass an increase was noted in the western part for most gadoid species. Several species that showed an increase in the western part also increased in the rest of the Oosterschelde, while for other species the decrease at one station was com-

pensated with an increase at another station. For example, both plaice and dab showed a decrease at stations 7 and 10, which was attributed to the strong yearclass of 1987. But this was partly compensated with higher densities and biomasses at station 5, which was probably related with an increased food resource. The western part of the Oosterschelde has become extremely important for the sublitoral farming of mussels, as >40% of all landings in 1996 were derived from the upper western part (van Berchum & Wattel 1997). For sole the difference in the western part was merely due to a shift from station 7 in 1987-'89 towards station 10 in 1999-2001. However, also in the western Wadden Sea an increased abundance of sole, flounder and herring was found in fyke catches taken between 1972 and 1994 (Philippart *et al.* 1996).

In the central part 7 species showed a decrease in density and biomass. Mainly species like herring, cod, viviparous blenny and 3-spined stickleback decreased in all stations of the central part in 1999-2001. Most probably, the latter species disappeared because it is more a fresh water species. In the Humber estuary (UK) 3-spined stickleback was mainly correlated with low salinities (Marshall & Elliott 1998), and in the Thames (UK) it was mainly found upstream (Araujo *et al.* 1999). This makes clear that 3-spined stickleback cannot tolerate the overall salinity of 30 psu in the Oosterschelde. But also in the adjacent Westerschelde estuary, no sticklebacks were caught in 1999-2001 (Chapter 9). In the Elbe estuary (Germany) the anadromous fish species (*e.g* ruffe, flounder, stickleback, eel and twaite shad) were the commonest species in 1989-'92 (Thiel *et al.* 1995). The few individuals of 3-spined stickleback that were caught in 1987-'89 (mainly in the western part) could be seen as relicts from the former estuarine populations. Most other anadromous species already had disappeared from the Oosterschelde before or during the engineering works (Doornbos *et al.* 1981, Chapter 3-Add.). Similarly, the freshwater dams could be the main reason for the decrease in adult eels.

In the central part 28 species increased. In contrast with the other subareas, 16 species showed an increased density at 4 or all 5 stations in this subarea in 1999-2001. For example, the six-fold increase in density of dragonet was noted both in the central and western part. Dragonet is known to be correlated with sandy bottoms (Froese & Pauly 2002), which was the case at most stations in the Oosterschelde (Chapter 5). But the highest densities were recorded at station 15 every year between 1999 and 2001, where the deposition of fine sediments (<50 µm) increased substantially after the construction of the storm-surge barrier (ten Brinke *et al.* 1994). In February 2000 the silt concentration even exceeded 50% at station 15 (Chapter 5). Between 1970 and 1986 this species was recorded as common during several years in the Oosterschelde (van Beek & Rink 1987), but the densities were not as high as in 1999-2001. Probably, juvenile dragonet could profit of the increase in its main food source, namely shrimps (and polychaetes) in this subarea (Chapter 5). The 'sudden' appearance of painted goby in November 2001 cannot easily be explained. Normally they prefer rocky bottoms in open coastal waters. According to divers, painted goby is not so uncommon in the Oosterschelde (P. van Bragt, www.anemoon.org). The higher densities of both nilsson's pipefish and greater pipefish at stations 15 and 21 could be related with the *Zostera* beds, which were still present in the central part (van Berchum & Wattel 1997). But nilsson's pipefish showed an increase in summer and autumn throughout the Oosterschelde in 1999-2001, which was most probably attributed to an increased net-efficiency. Mainly during these seasons a huge amount of allochtonous macrophytes (*Ulva* and *Chaetomorpha* species) came off the sublitoral mussel plots and clogged the nets, which prevented the pipefish from escaping.

In the eastern part 14 species showed an increased density and biomass and 5 species increased at all 3 eastern stations in 1999-2001. The changed net-efficiency and a sometimes excessive subsampling were probably the main reasons for the increased density of gobies and pipefish. On the other hand, 14 species had decreased in the eastern part. To reduce the risk of tearing the nets due to the presence of oysters or clogging of the nets with macrophytes, the beam trawl was usually swept over a distance <500 metres in this subarea. Both factors could have lead to a conversion discrepancy towards larger fish, but most probably the overwhelming presence of drifting algae and oysters in 1999-2001 reduced the habitat quality. This resulted in a substantial decrease both in density and biomass of all flatfish and gadoid species in the eastern part.

Also, at station 38 in the northern part the trawled distance was reduced to 500m, due to oysters or mud accumulation in the net. The silt concentration amounted to 50-65% in the northern area in 2000 (Chapter 5). With the exception of 12 uncommon species, most species that were found in the rest of the Oosterschelde also occurred in the northern part at comparable densities. For several species peak densities were recorded in the northern part, *e.g* herring and sprat at station 38, and sole, seabass, butterfish and viviparous blenny at station 37. Conversion discrepancies can only partly explain the higher densities. It is a pity the northern part was not sampled in the eighties in a comparable standardized way. However, this subarea was found to be important between 1960 and 1986 as well (Doornbos *et al.* 1981; van Beek & Rink 1987). The high densities in the northern part were probably related to a high food supply. On the large intertidal mudflat and sandbank in this area high biomasses were recorded for several mac-

robenthic organisms during the eighties (Seys *et al.* 1994). Also, the average density of hyperbenthic organisms in the subtidal station 38 was comparable with other subareas in 2000 (Chavatte 2001). Still, it is interesting to note that at several occasions the highest densities or biomasses of most fish species were recorded at those stations with a higher concentration of fine sediments (<53 µm), i.e. station 10 in the western part, station 21 near the closed Veerse Meer in the central part, station 15 towards and stations 37 and 38 in the northern part. This result again proved the importance of sediment or substratum type (Chapter 2-Add.2) in the spatial distribution of fish assemblages. On the other hand, the appearance of black goby in the eastern and northern part of the Oosterschelde was possibly due to a colonisation through sluices from the adjacent lakes. This was most probably also the case for the few recordings of smelt and twaite shad, which were only recorded from the northern part.

4.5 Final conclusion

From this study it was not possible to say what happened in between the periods 1987-'89 and 1999-2001, nor to say anything about a possible decrease in elder individuals or about pelagic and other species, which are difficult to catch with a 3-metre beam trawl. But, this study made clear that the Oosterschelde still harbours a species-rich fish fauna, with a spatio-temporal increase in density and biomass in most parts of the Oosterschelde for several juvenile fish species. This only had a minor influence on the nursery and feeding function of the ecosystem, except for the eastern part, where the fish fauna probably will not return to a better state of homeostasis in the near future as a consequence of man-induced, but also non-irreversible, changes.

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CHAPTER 4 - ADDENDUM THE EBB-TIDAL DELTA OF THE GREVELINGEN: A MAN-MADE NURSERY FOR FLATFISH?

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Abstract. *In order to investigate the impact of the closure of the Grevelingen estuary on the benthic life and the nursery function of its ebb-tidal delta, a comparison was made between the present ebb-tidal deltas of the Grevelingen and the Eastern Scheldt. Three groups of benthic animals were compared: macrobenthos, epibenthic animals (including demersal fish) and hyperbenthos. The ebb-tidal delta of the Grevelingen is much richer for almost all animal groups discussed. The data suggest that this richness is a consequence of the changes that have occurred in the hydrodynamics since the closure of the Grevelingen estuary in 1971. The area now traps and retains mud, detritus, larvae of different groups of infaunal animals, larvae of epibenthic crustaceans, and eggs and larvae of fish. This change is reflected in the increased importance of the area as a nursery for flatfish, especially dab and sole. However, the increase in the nursery function of the ebb-tidal delta does not make up for the loss of nursery areas in the estuary itself.*

4.1 Introduction

Three main European rivers, the Rhine, the Meuse and the Scheldt, enter the North Sea in the so-called Delta area in the southwest of the Netherlands. Prior to 1970, four main estuaries existed in the area from north to south: the Haringvliet, the Grevelingen, the Eastern Scheldt and the Western Scheldt.

The storm flood of 1953, which inundated 1500 km² of land and caused the death of nearly 2000 people, led the Dutch government to adopt the Delta plan in 1957. In this scheme, the Haringvliet was closed in 1970 and is now a freshwater basin. The Grevelingen estuary was closed in 1971 and is now a saline lake. The Eastern Scheldt is maintained as a tidal marine embayment protected by a storm-surge barrier completed in 1986. Only the Western Scheldt remains as a typical tidal estuary. A description of the ecology of the different estuaries before the engineering works started is given in Wolff (1973). The present situation is summarized in Heip (1989b).

It was soon apparent that the engineering works not only affected the (former) estuaries on the landward side, but that there was also an impact on the ebb-tidal deltas on the marine side of the dams. Important changes have occurred in the hydraulic conditions and the geomorphology of the Voordelta (the shallow coastal area in front of the dams and (former) estuaries (Kohsiek 1988a)). These changes have been studied in detail in the ebb-tidal delta of the Grevelingen (Louters *et al.* 1991). There has been a net erosion of the delta front and the relic tidal shoals, and a net sedimentation in the tidal channels

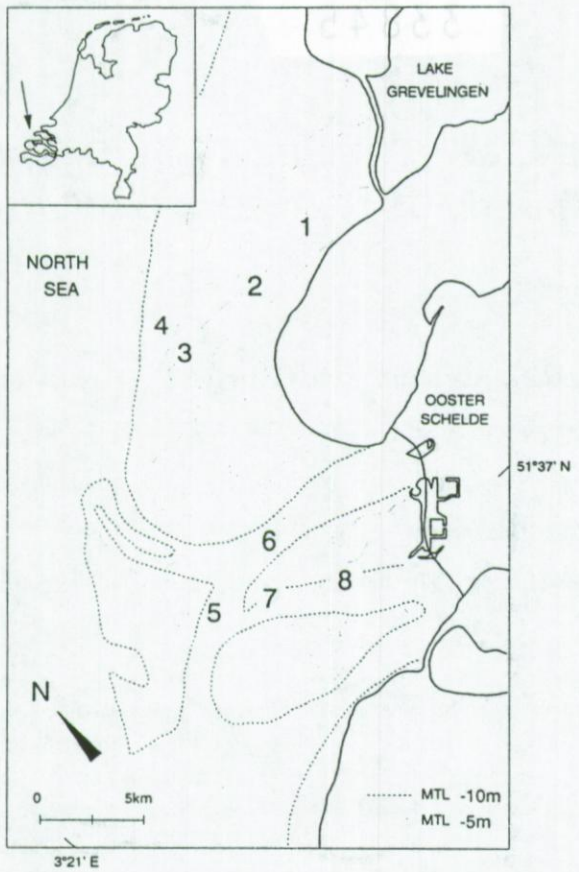

Fig. 4.7 Map of the study area with the sampling localities for the epi- and hyperbenthos

and at the longshore bars near the seaward edge of this ebb-tidal delta.

Within the framework of an integrated research project, several biotic components of the Voordelta have been studied in conjunction with the geomorphological studies (Mulder *et al.* 1991). These studies were centred on the ebb-tidal deltas of the Grevelingen and the Eastern Scheldt. The rate of change in the ebb-tidal delta of the Grevelingen has slowed down and the area is now geomorphologically close to equilibrium. The aim of the research project was to predict the changes expected in the ebb-tidal delta of the Eastern Scheldt after the completion of the storm-surge barrier, on the basis of the observed changes in the ebb-tidal delta of the Grevelingen.

The meiofauna was studied in 1984-1985 (Heip *et al.* 1990, Vanreusel 1990, Vanreusel 1991) but will not be considered here. The macrobenthos of the Voordelta was studied from 1984 through 1988. A total of 861 stations were sampled. Multivariate analysis of these samples yielded six communities (Craeymeersch *et al.* 1990). The spatial distribution of these communities is relatively stable over time, though the abundance of the individual species fluctuates strongly (J.A. Craeymeersch, unpublished data). In the ebb-tidal deltas of the Grevelingen and the Eastern Scheldt, the macrobenthic was sampled in 1987 and 1988; the epibenthos and demersal fish (Arellano 1991) and the hyperbenthos (Hamerlynck & Mees 1991) were studied from mid-1988 through 1989. Some older data on the macrobenthos exist (Wolff 1973) but are not available in a format that allows comparison with the more recent data.

In this study, a comparison is made between the ebb-tidal deltas of the Grevelingen and the Eastern Scheldt. Aspects relevant to the nursery function of this part of the Voordelta were selected from other studies on the macrobenthos, the epibenthos and demersal fish and the hyperbenthos. An attempt is made to relate these results to the physical environment which has been substantially altered by human activities. As for most of these animal groups, historical data on the situation prior to the closure of the Grevelingen are absent; therefore, the ebb-tidal Eastern Scheldt is taken as a model of the situation in the ebb-tidal delta of the Grevelingen estuary as it was before 1971. In this way, the large-scale experiment conducted by the closure of the estuaries of the Dutch Delta may shed some light on the factors involved in the 'creation' of nursery areas.

4.2 Material and methods

4.2.1 Study area

The study area proper covers the central part of the Voordelta (Fig. 4.7). The Voordelta is the shallow coastal area formed by the interlinked ebb-tidal deltas of the (former) estuaries of the Dutch Delta. It stretches from the Belgian-Dutch border in the south to De Hoek in the north. Its marine boundary is arbitrarily defined by the –10 m MTL (Mean Tidal Level as defined for Amsterdam) depth contour and extends 10 to 15 km seaward from the coastline. The tidal currents run parallel to the coast, the mean tidal range is 2.4 m, the average significant wave height at 21 m depth is 1.2 m and the major component of wave energy flux is from southwest to west (Louters *et al.* 1991).

This study centres on a comparison between the ebb-tidal deltas of the Grevelingen and the Eastern Scheldt, the latter serving as a proxy for the ebb-tidal delta of the Grevelingen as it existed in 1970 prior to the closure. Most of the important differences in environmental conditions in both ebb-tidal deltas are the result of the engineering works (*e.g* maximum current velocities, mud content and wave impact as measured by the 1%-significant wave: the wave height that is exceeded for 1 % of the time). Some small differences may have been present before 1970 but have become larger as a result of the works (*e.g* salinity, chlorophyll content and seston content). Two important differences were present before 1970. First, the median grain size of the sand fraction was

Table 4.5 Comparison of the ebb-tidal delta of the Grevelingen with the ebb-tidal delta of the Eastern Scheldt for a number of relevant environmental variables (mean ± standard deviation)

	Grevelingen	*Eastern Scheldt*	*sources*
Bottom			
mud content (%)	4.5±6.5	2.4±3.1	DIJKE & BUIJS, 1987
med. grain size (µm)	203±55	264±56	DIJKE & BUIJS, 1987
Water			
seston ($mg \cdot dm^{-3}$)	16±1	22±2	DIJKE & BUIJS, 1987
chlorophyll *a* ($\mu g \cdot dm^{-3}$)	10±2	9±1	DIJKE & BUIJS, 1987
salinity (ppt)	30.9±1.1	31.8±0.6	Mees (unpubl.)
Hydrodynamics			
max. current ($m \cdot s^{-1}$)	0.5±0.1	1.1±0.1	DIJKE & BUIJS, 1987
1% wave (m)	2.1±0.3	2.4±0.5	DIJKE & BUIJS, 1987
max. depth gully (m)	14	23	MULDER *et al.*, 1991

smaller in the ebb-tidal delta of the Grevelingen; and second, the depth of the tidal gullies was greater in the Eastern Scheldt (Kohsiek 1988b, van Dijke & Buijs 1987). The differences are summarized in Table 4.5.

Because of the building of the dam in the mouth of the Grevelingen estuary, the maximum current velocities in the tidal channel were reduced by 45 to 80 %. This led to the deposition of 30 10^6 m^3 of sediment in the ebb-tidal delta of the Grevelingen between 1970 and 1987 (Louters *et al.* 1991). About 10 to 30 % of this sediment is marine mud that settled mainly in the tidal gullies. Since 1987, similar developments have been occurring in the ebb-tidal delta of the Eastern Scheldt, though the changes are expected to be less significant because maximum current velocities have only been reduced by about 30 % (Mulder *et al.* 1991). The longshore sandbar that now exists in the ebb-tidal delta of the Grevelingen protects the area from wave action and contributes to the present lagoon-like nature of the area.

The influence of the Rhine on the Voordelta has increased since 1970. During strong northwesterly winds, a substantial input of nutrient-rich brackish water can move southwards along the coast as far as the mouth of the Eastern Scheldt. This influence probably accounts for the higher chlorophyll content of the water towards the north (Kohsiek 1988b).

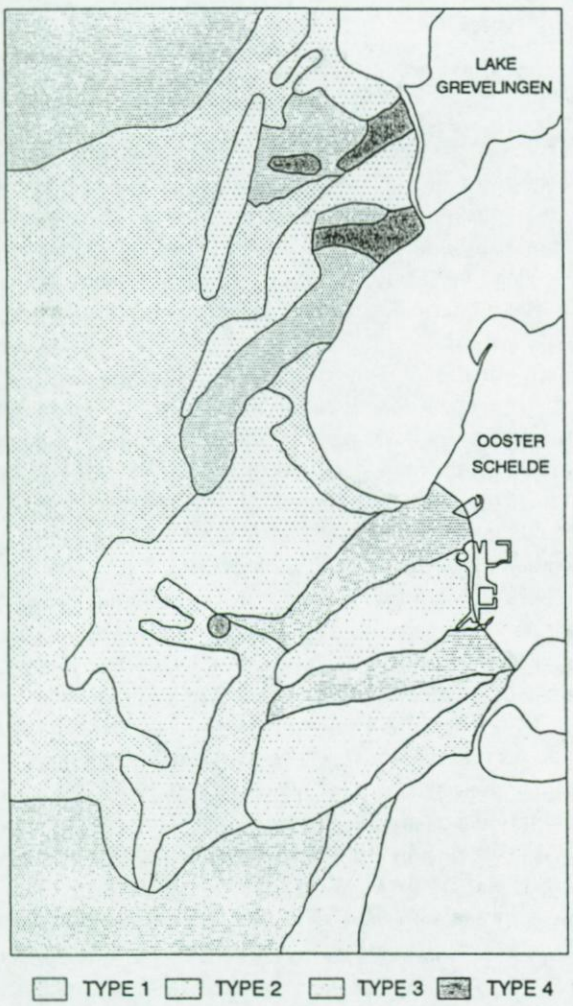

Fig. 4.8 Spatial distribution of the four macrobenthos community types in the study area

4.2.2 Sampling and data processing

For the purpose of this paper, a selection was made from available data. Only the 1988 sampling was considered from the data set on the macrobenthos because of its proximity in time to the epi- and hyperbenthic data collection. Annual mean density and biomass could only be calculated for the epibenthos and demersal fish for 1989 due to incomplete sampling in 1988, and only the peak densities of the eggs and larval stages for a number of hyperbenthos animal groups recorded in the spring of 1989 are reported. These data are primarily used as an index of the supply of larval and juvenile animals to the two areas.

Macrobenthos

In the autumn of 1988, samples were taken with a van Veen grab and sieved over a l-mm mesh at 125 stations. These were partitioned over the ebb-tidal deltas of the Grevelingen (N=62) and the Eastern Scheldt (N=63). Ash-Free Dry Weight (AFDW) was measured as the difference between dried (70°C for at least 48 hours) and ashed (520°C for 4 hours)

weights of the samples. The AFDW determined for molluscs included the shells.

The multivariate analysis classifies these samples into four different communities (Craeymeersch *et al.* 1990). The spatial extent of these communities within the study area is shown in Fig. 4.8. Within these four community types, mean macrobenthic biomass and standard errors (s.e.) were calculated, in each of the ebb-tidal deltas, for the macrobenthic taxa present. For details of the sampling procedure and data processing see Craeymeersch *et al.* (1990).

Epibenthos and demersal fish

During 1989, monthly samples were taken at eight localities: four each in the ebb-tidal deltas of the Grevelingen and the Eastern Scheldt (numbers 1 to 4 and 5 to 8 in Fig. 4.7, respectively). Two depth strata (MTL -5 m and MTL -10 m) were sampled in each locality. These strata were selected since deeper gullies have virtually disappeared from the ebb-tidal delta of the Grevelingen. Samples were taken from the R.V. "Luctor" (34 m, 370 kw) using a 3-m beam trawl, equipped with a 6-m long net with a 5x5 mm mesh in the cod end, a tickler chain and a chain in the ground rope. Trawls were 1 km in length and trawling speed relative to the bottom averaged 8 km h^{-1}.

The standard length was recorded for all fish specimens. Biomass was calculated from Length - Ashfree Dry Weight (AFDW) regressions compiled for the Delta area by K. Hostens (see Table 4.2). Invertebrates were counted and (wet)weighed. Net efficiency was assumed to be 20 % for all size classes of fish and invertebrates, an assumption based on the work of Kuipers (1975) on plaice. Efficiency for the relatively immobile starfish was assumed to be 40 %. For more details on the sampling procedure and data processing, see Chapter 3.

The abundance of juvenile flatfish in September, when most of the O-group have left the tidal flats (Pihl 1989, van der Veer *et al.* 1990b), is used as an index for the nursery function of the area.

Hyperbenthos

Concomitant with the sampling of the epibenthos, a hyperbenthic sledge with a 1xl mm mesh in the codend was deployed on the starboard side of the vessel. It sampled the lowest 1 m of the water column. The samples were sieved over a l-mm mesh and stored in jars with 7 % formalin. The gear is primarily designed for the sampling of the permanent members of the hyperbenthos, notably mysids and amphipods, however, in spring it also captures large quantities of fish eggs and larvae, larval decapods and some of the large pre-settlement stages of polychaete worms. For details of the gear, the sampling procedure and data processing, see Hamerlynck & Mees (1991). Only the peak abundances (means per area), occurring in May for fish eggs and larvae and in June for macrobenthos larvae and decapod larvae, are presented here.

Statistical analysis

All the density and biomass data of the different animal groups from both ebb-tidal deltas were first transformed to their natural logarithm to approximate normality and achieve homogeneity of the variances. Homogeneity was verified by the Bartlett test (Sokal & Rohlf 1981). The macrobenthos and hyperbenthos data were then subjected to a single classification Analysis of Variance (ANOVA). The epibenthos data were subjected to a two-way ANOVA with the area (Grevelingen *versus* Eastern Scheldt) as the first factor and the month of sampling as the second factor (Sokal & Rohlf 1981). Only the results for the first factor are discussed in this paper. The second factor is linked to the seasonal structure in the data. In temperate areas, the large difference between summer and winter densities accounts for a large part of the variance in the annual means and this conceals the differences between the two areas.

4.3 Results

4.3.1 Macrobenthos

Data for the macrobenthos of both ebb-tidal deltas are shown in Fig. 4.9 and Table 4.6. The first community (type 1) is restricted to the shallow sandy areas of both ebb-tidal deltas (number of stations N=l4 in the ebb-tidal delta of the Grevelingen, N=39 in the Eastern Scheldt). It is very poor (biomass in autumn less than 2 gAFDW m^{-2}), typical species are burrowing amphipods of the genus *Bathyporeia*.

The second community (type 2) is found mainly in the outer parts of the tidal gullies. Outside of the study area it covers most of the rest of the Voordelta in the areas of intermediate depth (Craeymeersch *et al.* 1990). It is richer than the first community with a mean biomass of 14 gAFDW m^{-2} (N=19, s.e. 5.6 gAFDW m^{-2}) in the ebb-tidal delta of the Grevelingen and 6 gAFDW m^{-2} (N=18, s.e. 3.1 gAFDW m^{-2}) in the ebb-tidal delta of the Eastern Scheldt. Typical species include *Nephthys cirrosa*.

The third community (type 3) covers the inner part of the tidal gullies with the exception of those areas where mud contents <10 %. It is a rich community with 34 gAFDW m^{-2} (N=21, s.e. 15.4 gAFDW m^{-2}) in the ebb-tidal delta of the Grevelingen and 24 gAFDW m^{-2} (N=4, s.e. 16.8 gAFDW m^{-2}) in the ebb-tidal delta of the Eastern Scheldt. Typical species include *Tellina fabula*, *Magellona papillicornis*, *Spiophanes bombyx* and *Lanice conchilega*.

Table 4.6 Comparison of the ebb-tidal delta of the Grevelingen with the ebb-tidal delta of the Eastern Scheldt and the F-statistic of the ANOVA and its significance level for the four macrobenthic community types, the main groups of epibenthic animals and the peak densities of the relevant hyperbenthic groups

	Grevelingen	*Eastern Scheldt*	*ANOVA F*	*significance level*
Macrobenthos total biomass (g AFDW·m⁻²)				
type 1	1.5	1.8	0.04	N.S.
type 2	14.0	6.0	5.8	$p < 0.05$
type 3	34.0	24.0	0.1	N.S.
type 4	32.0	8.3	-	-
Epibenthos density (N·m⁻²)				
total density	7.0	1.8	41.0	$p < 0.001$
other fish	0.7	0.2	43.9	$p < 0.001$
flatfish	0.11	0.06	0.9	N.S.
shrimp	2.2	0.9	8.1	$p < 0.01$
crabs	0.3	0.1	12.5	$p < 0.001$
starfish	3.7	0.5	46.8	$p < 0.001$
Epibenthos biomass (g AFDW·m⁻²)				
total biomass	9.9	2.4	29.3	$p < 0.001$
other fish	0.5	0.3	6.0	$p < 0.05$
flatfish	0.6	0.7	0.8	N.S.
shrimp	0.6	0.2	9.2	$p < 0.01$
crabs	0.7	0.2	7.5	$p < 0.01$
starfish	7.6	1.1	46.2	$p < 0.001$
Hyperbentos density (N·m⁻²)				
fish eggs (May)	1.8	0.4	5.3	$p<0.05$
fish larvae (May)	0.7	0.3	0.3	N.S.
macrob. larvae (June)	11.9	2.4	8.5	$p<0.05$
decap larvae (June)	21.2	15.0	1.6	N.S.

The fourth community (type 4) is restricted to the more muddy areas of the ebb-tidal delta of the Grevelingen (N=8, mean biomass 32 gAFDW m^{-2}, s.e. 16.9 gAFDW m^{-2}) and a small patch in the ebb-tidal delta of the Eastern Scheldt (N=2, 8 gAFDW m^{-2}). Typical species are similar to community type 3 but the relative proportions differ.

It is clear (Fig. 4.8) that the richest community, type 3, covers a relatively larger part of the ebb-tidal delta of the Grevelingen than that of the Eastern Scheldt and that macrobenthic biomass, within community type 2, is significantly higher in the ebb-tidal delta of the Grevelingen (Table 4.6).

4.3.2 Epibenthos and demersal fishes

The annual mean density of epibenthic animals is about four times higher in the ebb-tidal delta of the

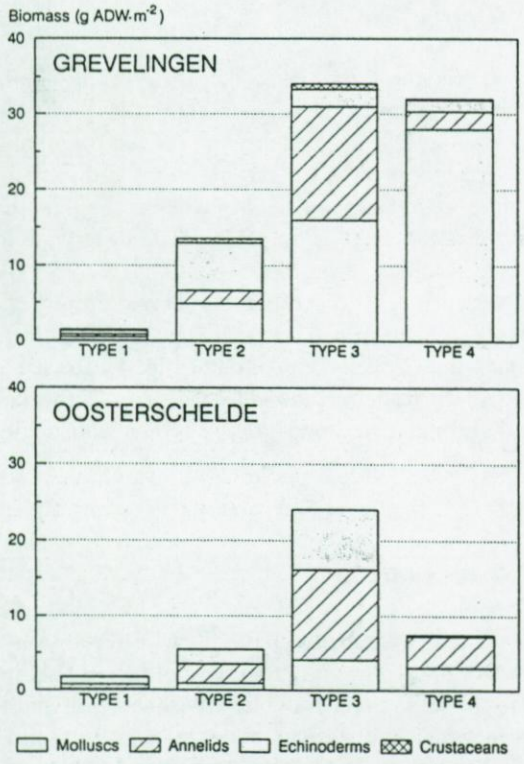

Fig. 4.9 Biomass composition of the four macrobenthos community types in the ebb-tidal deltas of the Grevelingen (top) and the Oosterschelde (bottom)

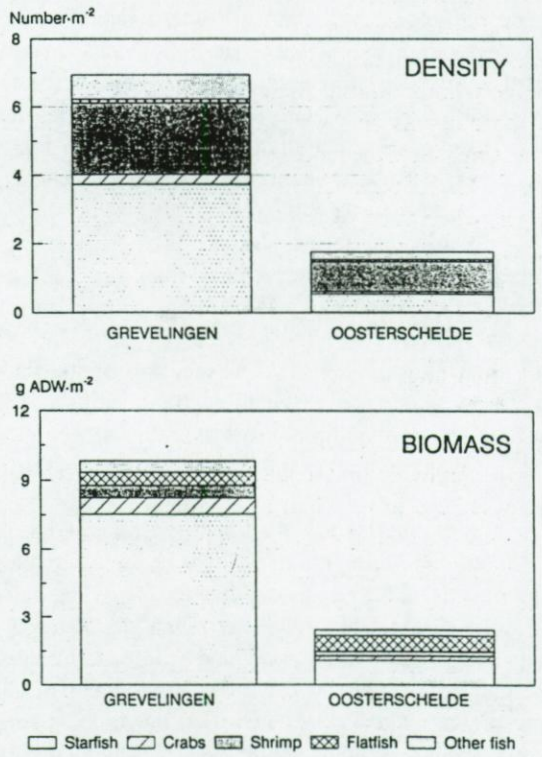

Fig. 4.10 Annual mean density (top) and biomass (bottom) composition for the epibenthos in the ebb-tidal deltas of the Grevelingen and the Oosterschelde

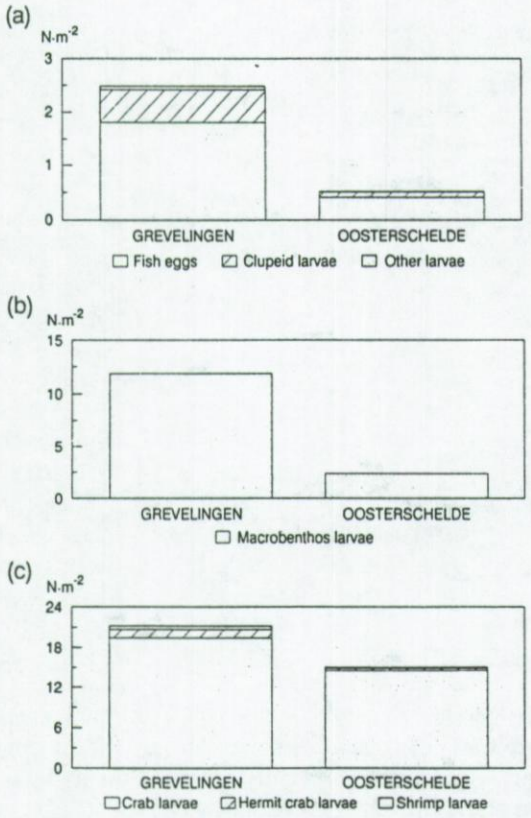

Fig. 4.11 Peak densities of the main groups of the temporary hyperbenthos in both ebb-tidal deltas: (a) fish eggs and larvae (May 1989); (b) macrobenthos larvae (June 1989); (c) decapod larvae (June 1989)

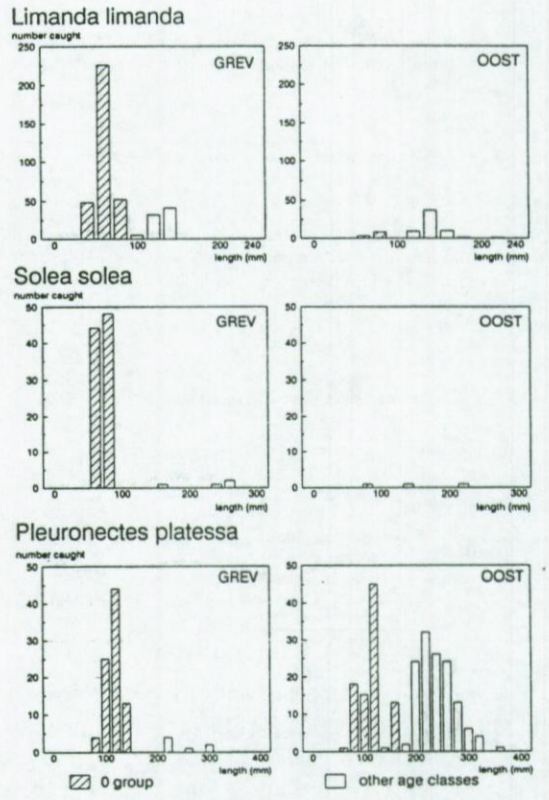

Fig. 4.12 Length-frequency distributions of flatfish caught in both ebb-tidal deltas in September 1989

Grevelingen than in the same strata sampled in that of the Eastern Scheldt (Fig. 4.10, Table 4.6). All major epibenthic groups are at least twice as abundant in the Grevelingen as in the Eastern Scheldt. For the crabs (mainly *Carcinus maenas* and *Liocarcinus holsatus*) and the starfish (*Asterias rubens*), densities are four and seven times higher, respectively. All these differences, with the exception of the flatfish (N.S.), are highly significant (Table 4.6).

In biomass terms, the ebb-tidal delta of the Grevelingen is four times richer than the Eastern Scheldt delta (Fig. 4.10, Table 4.6). Annual mean biomass is higher in the Grevelingen delta for all major species groups with the exception of the flatfish where the Eastern Scheldt delta sustains a 1.2 times higher biomass (N.S.). All the other differences are significant at the $p<0.05$ level or more (Table 4.6).

A comparison of the length-frequency distributions of the three main flatfish species between both ebb-tidal deltas is shown in Fig. 4.12. The ebb-tidal delta of the Grevelingen is much richer for O-group dab *Limanda Limanda* and sole *Solea solea*. Both ebb-tidal deltas have similar abundances of O-group plaice *Pleuronectes platessa*, but older plaice are much more abundant in the Eastern Scheldt delta.

4.3.3 Hyperbenthos

A comparison of the peak densities of the main groups of the temporary hyperbenthos is shown in Fig. 4.11. In May, fish eggs (mainly *Solea solea*) and larvae (mainly herring *Clupea harengus* and flatfish) are more abundant in the Grevelingen than in the Eastern Scheldt delta (Fig. 4.11a). The difference in fish egg densities is significant ($p<0.05$; Table 4.6). In June densities of macrobenthic larvae (almost exclusively *Lanice conchilega*) are nearly five times higher in the Grevelingen ($p<0.05$; Fig. 4.11b, Table 4.6). The difference in the peak densities of the larvae of the main decapod groups is not statistically significant (Fig. 4.11c, Table 4.6).

4.4 Discussion

There is still no consistent theory with testable hypotheses of how egg and larval mortalities in fish are related to the biotic and abiotic environmental conditions to which the animals are exposed (Rothschild 1986). For a few decades, the emphasis has been either on predation or on starvation as the limiting process (reviews in Leggett 1986, Cushing 1990).

The importance of physical processes in controlling population and community dynamics of marine systems has recently come into focus (Roughgarden *et al.* 1987, Doherty & Williams 1988, Sinclair 1988, Barry & Dayton 1991).

The present ebb-tidal delta of the Grevelingen is much richer for almost all benthic life than the ebb-tidal delta of the Eastern Scheldt. This is probably related to the fact that the area has become a 'sink' for different kinds of geological and biological material. Originally, the Grevelingen area may have been somewhat richer than the ebb-tidal delta of the Eastern Scheldt because of the slightly finer sandy bottom. Yet it is very likely that a considerable enrichment of the ebb-tidal delta of the Grevelingen has occurred for most benthic and epibenthic organisms as a consequence of the closure. The increased sedimentation of mud is well documented; the evidence for increased biological inputs to the area in the form of eggs and larval organisms is inferred from the evidence presented in this paper. The primary food source for the rich benthic life in the area, namely the sedimentation of detritus from phytoplankton blooms, is difficult to quantify (Smetacek 1984), but is likely associated with the sedimentation of fine particles such as mud. There is some anecdotal support for this contention from the visual aspect and the volume of the stored hyperbenthos samples: at the end of the phytoplankton bloom in the beginning of June (when the average Secchi depth increased from 1.8 m to over 4 m), the hyperbenthos samples from the Grevelingen area were characterized by a large volume (>2 dm^3) of brownish detrital material. In contrast, the samples from the ebb-tidal delta of the Eastern Scheldt were small (<250 cm^3) and transparent all year round (J. Mees, unpublished data). This suggests that the remains of the phytoplankton bloom (probably largely *Phaeocystis*, Reid *et al.* 1990) reach the sediments - and the benthic detritivores - in much larger quantities in the Grevelingen delta than in the more dynamic Eastern Scheldt delta.

Though the pelagic larvae of many benthic animals have the capacity to make selective use of currents, passive processes are important (review in Butman 1987). Hydrodynamic processes control the distribution of larvae over the bottom, causing aggregation of passive and swimming larvae on several spatial scales (Barry & Dayton 1991). In the case of the ebb-tidal delta of the Grevelingen, it could be argued that the relative richness in *L. conchilega* larvae is caused by the larger adult populations present there. However, the larvae caught in the hyperbenthic sledge are the tubed aulophore stage ready for settlement. These have been present in the plankton for three to six weeks (Bhaud 1988). Thus, even if the larvae are derived from local production, they have been retained in the area for a considerable stretch of time. Similarly, the eggs of *Solea solea* may come from a small local spawning population. Still, it is more likely that they were transported with the residual current (van Alphen 1990) from the important spawning ground along the Belgian coast (Rijnsdorp *et al.* 1992), and that they were subsequently trapped in the ebb-tidal delta of the Grevelingen. Herring larvae are known to depend mainly on passive drift for their transport from spawning to nursery grounds (Cushing 1986). Flatfish larvae are passively transported by the tides (Bergman *et al.* 1989). The same holds for the decapod larvae (Sulkin 1984). In summary, though active mechanisms may play a role, the relative richness of the ebb-tidal delta of the Grevelingen for all these organisms is probably largely determined by the hydrodynamical properties of the system. It is intriguing that both ebb-tidal deltas are of equal importance as nurseries for plaice, which prefer sandy intertidal areas (van der Veer *et al.* 1990b). In the Voordelta, these areas coincide with the low biomass type-1 macrobenthic community whose composition is virtually identical in both ebb-tidal deltas.

The observation that the ebb-tidal delta of the Grevelingen, having changed from a purely sandy area scoured by strong tidal currents to a sink for mud, now has an increased nursery function for flatfish is supported by a similar observation in the marine bay that was formed on the landward side of the Eastern Scheldt storm-surge barrier (the Eastern Scheldt proper). In this former estuary, the reduction of current velocities caused sedimentation of mud in the northwestern part. This was correlated with an increase of flatfish densities there (Chapter 3).

Sedimentation and entrapment may be neither necessary nor sufficient conditions for a successful flatfish nursery. The selective use of tidal currents by pelagic stages of both invertebrates (Wooldridge & Erasmus 1980, Butman 1987) and vertebrates (De Veen 1978, Rijnsdorp *et al.* 1985) is well documented. This allows the animals to remain stationary or even move against the residual current which means nurseries are not necessarily situated in 'sinks'.

On the other hand, the sedimentation area associated with the gyre in front of the Belgian coast (Nihoul & Ronday 1975) is almost devoid of benthic life, except for a few nematode species (Vincx & Herman 1989). It is still not clear if this is only due to the extremely high mud content of the sediment or if there is an additional effect of pollutant toxicity. In the less polluted Voordelta, the stations (from the 861 station data set) with mud contents >50 % also have an impoverished macrobenthic fauna with <2 gAFDW m-2 (Hamerlynck & Craeymeersch 1990).

Another limiting factor to the nursery function of areas with high nutrient inputs and an important sedimentation of the phytoplankton bloom may be the anoxic conditions that can develop and are detrimental for benthic life forms (see Rosenberg &

Loo 1988). 'Sinks' are therefore not necessarily good nurseries. A sink with some undefined intermediate level of hydrodynamics seems most appropriate for the development of a nursery ground. The prime importance of the Wadden Sea as a nursery for flatfish (van Beek *et al.* 1989) may be related to the same hydrodynamical features outlined for the ebb-tidal delta of the Grevelingen, though on a much larger scale.

Pearson & Rosenberg (1987) contend that food availability is the single most important factor structuring benthic communities. In apparent contrast to this contention, Roughgarden *et al.* (1987) emphasize the importance of physical transport processes for larval supply. These views can be combined into one for the benthic and epibenthic fauna in the ebb-tidal deltas of the Grevelingen and the Eastern Scheldt: the extant current pattern supplies the ebb-tidal delta of the Grevelingen both with more larval organisms and with more food. Part of this higher food supply may be caused by a higher local primary production, due to the higher nutrient input from the Rhine to the more northerly ebb-tidal delta. Still, the current pattern allows this primary production to be used locally. This local production is most probably supplemented by detrital material originating from the phytoplankton bloom of a much wider area.

Unfortunately, there are no previous flatfish density data for the part of the Grevelingen estuary that became the ebb-tidal delta. The Demersal Young Fish Survey (DYFS) (van Beek *et al.* 1989, Daan *et al.* 1990) only started in 1970. In the autumn of 1971, a few months after the closure, it was estimated that the O-group plaice density in the saline Lake Grevelingen was about 0.13 per m^2 (Doornbos & Twisk 1984). Assuming that the relative abundances of plaice *versus* sole and dab were similar in 1970 (DYFS data) and 1971, correcting for year-class strength of plaice and sole (Rijnsdorp *et al.* 1991) and for abundance level changes in dab (Tiews 1990) and assuming net efficiency of the DYFS is only half as efficient as the beam trawl used in this study (because it uses bobbins in the ground rope instead of a chain), a rough calculation suggests that the increased importance of the ebb-tidal delta of the Grevelingen as a nursery can only compensate for 3 %, 5 % and 8 % of the loss entailed by the closure of the Grevelingen estuary for sole, plaice and dab, respectively.

4.5 Conclusion

The closure of the Grevelingen estuary has resulted in a change in the current patterns on the marine side of the dam. Current velocities have been reduced substantially and a sand bar, protecting the area from wave action, has developed. This has created an environment which traps mud, detritus and eggs and larval stages of a range of marine organisms. In a sense, the increased nursery function of the marine part of the former ebb-tidal delta synthesizes all these changes: the animals are transported to the area as eggs or larvae and find a rich food supply. Both their initial food, the meiofauna, and their subsequent prime energy source, the macrofauna, thrive on the organic matter trapped by the same current pattern that brought the larvae there. However, if one balances the loss of nursery function on the landward side of the dam with the increased nursery function on the marine side, probably only a small part of the nursery function of the whole Grevelingen estuary including the ebb-tidal delta has been preserved.

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CHAPTER 5 THE MOBILE MACRO-INVERTEBRATE FAUNA OF THE OOSTERSCHELDE AND THE WESTERSCHELDE (SW NETHERLANDS)

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Key words: echinoderm, caridea, shrimp, prawn, brachyura, anomura, crab, lobster, cephalopod, estuary

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Abstract *Both in the marine bay the Oosterschelde and in the Westerschelde estuary, the mobile macro-invertebrate fauna from subtidal soft substrates was sampled with a three-metre beam trawl during 10 quarterly surveys between August 1999 and November 2001. A total of 35 species was recorded. In the Oosterschelde 33 species were found: 9 caridean prawns, 9 brachyuran crabs, 6 echinoderms, 3 caridean shrimps, 3 cephalopods, 2 anomuran crabs and 1 lobster. The dominating species in the Oosterschelde were brittlestar Ophiura species, brown shrimp Crangon crangon, starfish Asterias rubens, shore crab Carcinus maenas and hermit crab Pagurus bernhardus. Diversity in the Westerschelde was much lower, with only 8 species recorded (4 brachyuran crabs, 2 caridean prawns, 1 caridean shrimp, and 1 anomuran crab) and an overall dominance of Crangon crangon. The main abiotic factors influencing the macro-invertebrate diversity patterns were salinity, sediment/habitat type and temperature. In contrast to the Oosterschelde, the Westerschelde population of Carcinus maenas was not infected with the parasitic barnacle Sacculina carcini. In both systems introduced alien species (mainly crabs) occurred. Arch-fronted swimming crab Liocarcinus arcuatus outnumbered the local populations of flying crab Liocarcinus holsatus in the Oosterschelde. This is possibly related to the reproductive success of L. arcuatus, as seen from the difference in sex ratio between both species in winter (3:1 females in L. arcuatus versus 2:1 males in L. holsatus). The sex ratio in Carcinus maenas and Liocarcinus depurator did not differ from 1:1, and respectively 30% and 100% of the females bore eggs in spring. In the near future these species might suffer the invasion of japanese brush crab Hemigrapsus penicillatus. At the end of the 1990s, the total average density amounted to 3500 and 1600 individuals per 1000 square metres in the Oosterschelde and Westerschelde, respectively; total average biomass was 1700 and 240 gram ashfree dryweight per 1000 square metres. The seasonal distribution was related to the annual patterns in temperature and dissolved oxygen concentration. The (re)occurrence of Palaemon longirostris in the Westerschelde possibly reflects an improved water quality. A number of species stayed for a short period, while others were present in considerable densities throughout the year. Most of the smallest juveniles were recorded in spring and summer. Peak densities of 55 and 90% of the species were recorded during the warmer seasons in the Oosterschelde and Westerschelde, respectively. Only in the Westerschelde a spatial pattern in species composition was found to be related to the gradient in salinity and turbidity; three species reached higher densities in the eastern part of the estuary. Several macro-invertebrate species showed a high interannual variability. Higher densities were related to mild winters, the presence of abundant food resources, both sub- and intertidally, major engineering works, and presence of intertidal habitat.*

5.1 Introduction

At the end of the 1980s several sampling campaigns were performed to study the importance of the Oosterschelde and the Westerschelde as nursery and feeding grounds for demersal fish assemblages. During these juvenile fish surveys, the most conspicuous macro-invertebrates were also taken into account, as they generally form the main component of demersal epibenthic communities in estuaries, shallow coastal areas and surfzone beaches, both in terms of density and biomass (*e.g* Bamber & Henderson 1994, Beyst *et al.* 2002, Chapter 2-Add.2). It was estimated that at the end of the 1980s the subtidal area of the Oosterschelde (227 km²) held on average 9 10^7 *Crangon crangon*, 7 10^7 *Asterias rubens*, 1 10^7 *Carcinus maenas*, and 2 10^6 individuals of *Liocarcinus holsatus* (Hostens & Hamerlynck 1993, Chapter 3). Within the subtidal part of the Westerschelde (200 km²) the estimates amounted to 4 10^8 juvenile *C. crangon*, 3 10^6 *C. maenas*, and 8 10^5 *L. holsatus* (Chapter 2). Several hyperbenthic studies emphasized the presence of (post)larvae of different macro-invertebrate species, the so-called merohyperbenthos, in both systems (Cattrijsse *et al.* 1994, Mees 1994, Chavatte 2001). However, almost no scientific data on mobile macro-invertebrate diversity in the Dutch Delta area have been presented since the 1970s (Wolff 1968, Wolff & Sandee 1971, Heerebout 1974). The most recent published data on ophiuroids from soft sediments in the Oosterschelde were gathered during the 1970s (De Veen *et al.* 1979) and from hard substrates during the 1980s (Leewis *et al.* 1994). Since the completion of the major engineering works (the so-called Delta works) most of the estuarine branches in the Dutch Delta area have been altered (Heip 1989a). Also, macro-invertebrate diversity seems to have changed, with several new crab and caridean prawn species appearing in the Oosterschelde and the Westerschelde (Adema 1991b, d'Udekem d'Acoz & Faasse 2002). According to d'Udekem d'Acoz (1999) 3 problems jeopardize the decapod fauna throughout the world: habitat destruction or degradation, the introduction of alien species (which might compete with native species, introduce diseases or modify the habitat), and, for a limited number of species, overfishing.

The aims of this study are: (1) to describe the spatial, seasonal and interannual distribution patterns in diversity, density and biomass of all mobile macro-invertebrate species caught on subtidal soft substrates in the Oosterschelde and the Westerschelde during the end of the 1990s, (2) to compare these patterns with data available for the dominant species from the end of the 1980s, and (3) to evaluate the abiotic and biotic influences (including human impact) on these patterns.

5.2 Materials and methods

The Oosterschelde is a mesotidal marine oligotrophic bay without a salinity gradient, situated in the Southern Bight of the North Sea (the Netherlands). The total area covers 351 km² and the subtidal area amounts to 227 km² (Fig. 5.1). The Oosterschelde is characterized by multiple tidal channels, mudflats and large intertidal sandy shoals, and can be divided into four geographical subareas: the western (in the mouth), central, eastern (the basin) and northern (the branch) parts. The distance from the storm-surge barrier in the mouth to the Oesterdam in the east and to the Philipsdam in the north both equals 40 km. The extensive flats and the surrounding shallow subtidal areas in the Oosterschelde are especially used for shellfish farming, while the subtidal is intensively used for shipping and recreational activities. The ecological and environmental properties of the Oosterschelde are explained in detail in Nienhuis & Smaal (1994a) and van Berchum & Wattel (1997).

The Westerschelde is a macrotidal turbid and nutrient-rich estuary, with a marked salinity gradient. It is situated south of the Oosterschelde and connected directly with it through a channel between Hansweert (in the Westerschelde) and Yerseke (in the Oosterschelde), and indirectly through sluices in the Zoommeer (Fig. 5.1). The Westerschelde consists of the lower and middle parts of the Schelde estuary and covers 310 km² with 200 km² of subtidal area. The Westerschelde stretches along 55 km from the mouth (arbitrarily situated near Vlissingen) to the Dutch-Belgian border, and can be divided in two

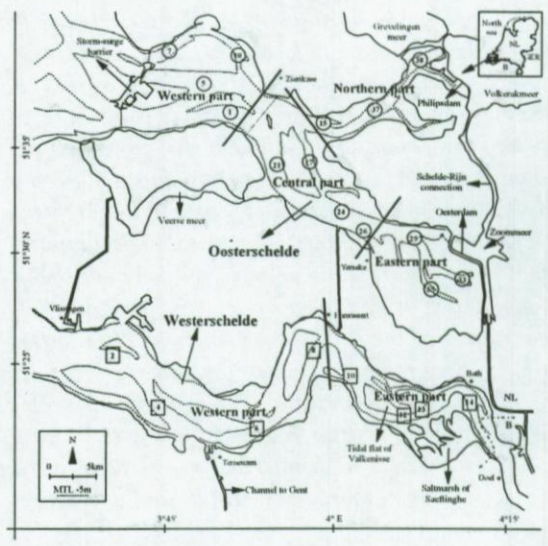

Fig. 5.1 Map of the study area with an indication of the sampling locations and the division in subareas in the Oosterschelde and the Westerschelde

Table 5.1 Overview of the used sampling surveys in 1999-2001, both in the Oosterschelde (14 stations) and the Westerschelde (8 stations), with a notification of those stations where the sampling distance was reduced from 1000 to 500 metres or less, and of the main 'bycatch' in the net during 1999-2001. Also, the corresponding surveys from 1988-89, used for the longterm comparison of 4 macro-invertebrate species, are given

survey 1999-2001	Samples with reduced distance Oosterschelde	Westerschelde	main bycatch during 1999-2001 (+ station number)	corresponding survey 1988-'89[3] Oosterschelde (Westerschelde)
30 Aug - 2 Sep 1999	29[1], 33[1], 35[1], 38[1]	14	macrophytes (all stations); peat (5), mussels (21), tunicates (37), mud (38)	-
22 - 26 Nov 1999	15, 35, 38	14	Ulva (10, 15, 26 to 35)	-
7-8, 16-17 Feb 2000	33, 35, 38	14	mud (10), peat (26), oysters (29 to 35)	5, 8, 11 (12) Feb 1988
15 - 18 May 2000	17, 24, 29, 33[2], 35[2], 38[2]	14	macrophytes & diatoms (29 to 35), tunicates (5, 15, 38), shells-Ensis (5, 17, 26)	13 - 14 Jul (18 May) 1988
28 - 30 Aug 2000	all, except 1 & 21	14	macrophytes (1, 15, 29 to 35, 37), cnidarians (21), tunicates (5)	23, 26 Sep (26 Aug) 1988
20 - 22 Nov 2000	33[2], 35, 38	14	macrophytes (21, 26, 33 to 35), tunicates (5), oysters (17, 29, 35, 38), Crepidula (29), Ensis (5, 17)	14 - 17 (8) Nov 1988
19 - 21 Feb 2001	33, 35, 38	10, 14	peat (24, 26, 35), ensis (5), mussels (26), oysters (29, 33, 38), Crepidula (33)	14 - 15 (6) Feb 1989
21 - 23 May 2001	1, 5, 7, 33[2], 35[2], 38	14	macrophytes (26, 29), peat (17), mud (15, 38), oysters (33, 35, 38), Ensis (5, 17), hydrozoa (37)	12 - 16 (18) May 1989
20 - 22 Aug 2001	26, 33[2], 35, 38[2]	14	Ulva (29 to 37), oysters (38), mussel spat (5)	7 - 8 (17) Aug 1989
19 - 21 Nov 2001	26, 33, 35, 38[2]	2, 14	no remarks	3 - 6 (15) Nov 1989

[1]100 metres, [2]250 metres; [3]no samples at station 37 & 38 in the Oosterschelde and no distance reductions

subareas: the western (marine) and eastern (brackish) part. The Westerschelde is characterized by multiple channels surrounding large intertidal flats, bordered by mudflats and a large saltmarsh in the eastern part. This ecosystem is under constant pressure of urban organic pollution and dredging activities for shipping purposes. The ecological and environmental properties of the Westerschelde estuary are explained in detail in Meire & Vincx (1993), Heip & Herman (1995) and Van Damme *et al.* (1999).

The macro-invertebrate fauna was sampled in the subtidal channels at an average depth of 13 (± 3) metres (range 7-21 m) below mean tidal level. A 3-metre beam trawl was equipped with one tickler chain, a chain in the ground-rope and a fine-meshed net (5*5 millimetres in the cod end). Ten quarterly surveys were conducted between August 1999 and November 2001, each with 14 samples in the Oosterschelde and 8 samples in the Westerschelde (Fig. 5.1). All samples were taken during daytime with the RV Luctor (34m, 500 Hp), generally within a 3-day period near spring tide. The beam trawl was towed over a distance of 1000 metres at an average speed of 4.5 knots relative to the bottom. At a number of stations trawling distance was reduced to 500 or fewer metres to prevent clogging or tearing of the nets by storm-torn macrophytes, oysters or mud (Table 5.1). Four environmental variables were measured at the end of each trawl: salinity (psu), temperature (°C), dissolved oxygen ($mg.l^{-1}$) and turbidity (calculated as the reciprocal of Secchi disc depth). The median grain size (µm) and silt concentration (%) were determined once at every station in February 2000.

The macro-invertebrate species were identified, counted and wet weighed, be it as a whole or as a weighed subsample. Caridean shrimps and prawns, brachyuran crabs and starfish *Asterias rubens* were measured to the nearest millimetre, the other crustaceans and echinoderms were not measured. Crabs were sexed and the infection rate of shore crab *Carcinus maenas* with the parasitic barnacle *Sacculina carcini* was noted. A number of sessile and planktonic invertebrate species were quite common in the samples from the Oosterschelde, but these were not taken into account: tunicates (a.o. *Styela clava, Ciona intestinalis* and *Ascidiella aspersa*), cnidarians (also in the Westerschelde, a.o. *Aurelia aurita*, *Chrysaora hysoscella* and *Cyanea lamarckii*), sea anemones (a.o. *Actinia equinea*), bivalves (*Mytilus edulis*, *Ostrea edulis* and *Crassostrea gigas*), gastropods (a.o. *Littorina littorea*, *Crepidula fornicata* and *Nucella lapillus*), polychaetes (a.o. *Aphroditae* and *Harmothoe* species), and nudibranchs (a.o. *Aeolidia papillosa* and *Elysia viridis*) were not quantified and excluded from further analyses.

Density was expressed as numbers per 1000 m^2, assuming an overall 20% net-efficiency (see Chapter 3). Biomass was calculated by means of length-weight regressions or number-weight conversions (Table 5.2), and was expressed in gram ashfree dryweight (ADW) per 1000 m^2. For the hermit crabs the gastropod shell was included in the conversions. Spatial and temporal patterns in the environmental variables and in species diversity, growth, density and biomass were compared between both systems. Two Canonical Correspondence analyses were performed on the fourth-root transformed data of the Oosterschelde and Westerschelde, respectively based on 139 and 80 samples, all species and 4 environmental variables. The multivariate procedure details were given in Chapter 2-Add.2 (also see §9.6.1).

A comparison was made with a reduced data set of four invertebrate species (*Asterias rubens, Crangon crangon, Carcinus maenas* and *Liocarcinus holsatus*) from 8 corresponding quarterly surveys, conducted during the period 1988 - 89 at the same sampling points in both systems except at stations 37 and 38 in the Oosterschelde (Fig. 5.1). More information on these surveys was given in Hostens *et al.* (1993), Chapter 2 and Chapter 4.

5.3 Results

5.3.1 Species richness

A total of 33 macro-invertebrate species was recorded from the Oosterschelde. On average 9 species were caught per sample and 15 species per subarea in every season, with the highest diversity in autumn and in the central part, and the lowest diversity in

Table 5.2 Species list and Frequency of Occurrence (FO%) in the Oosterschelde and Westerschelde (the latter between brackets). Length range (mm) given as body + one arm (BOA) for starfish, total length (TL) for caridean shrimps and prawns, carapax width (CW) for brachyuran crabs, and mantle length (ML) for cephalopods. Also, some number/length - wetweight (WW) conversions are given. Ashfree dryweight (ADW) equals 20% of the wetweight

Taxon – Species	FO% OS (WS)	length range (mm) OS (WS)	WW conversions (gram)
Echinodermata - Asteroidea (starfish)			
Asterias rubens L., 1758	96	5-165	WW=13.27*Number
Echinodermata - Ophiuroidea (brittlestars)			
Ophiothrix fragilis (Abildgaard, 1789)	33		WW=1.04*Number
Ophiura albida Forbes, 1839	70		WW=0.40*Number
Ophiura ophiura (L., 1758)	70		WW=1.14*Number
Echinodermata - Echinoidea (sea-urchins)			
Echinocardium cordatum (Pennant, 1777)	12		WW=50.21*Number
Psammechinus miliaris (Gmelin, 1778)	37		WW=22.10*Number
Crustacea - Caridea (shrimps)			
Crangon allmanni Kinnagan, 1857	1	33-39	
Crangon crangon (L., 1758)	97 (100)	15-71 (16-74)	WW=0.87*Number lnWW= -10.434+2.686*lnTL (n=165, r^2=0.98)
Philocheras trispinosus (Hailstone, 1835)	8	13-25	
Crustacea - Caridea (prawns)			
Athanas nitescens (Leach, 1814)	1	20	
Hippolyte varians Leach, 1814	4	18-28	
Palaemon adspersus Rathke, 1837	9	31-66	
Palaemon elegans Rathke, 1837	6	29-67	
Palaemon longirostris H. Milne-Edwards, 1837	2 (44)	42-56 (25-67)	
Palaemon serratus (Pennant, 1777)	14	36-90	
Pandalina brevirostris (Rathke, 1843)	3	27-32	
Pandalus montagui Leach, 1814	12 (4)	30-65 (50-67)	
Thoralus cranchii (Leach, 1814)	1	18	
Crustacea - Brachyura (crabs)			
Cancer pagurus L., 1758	2	95-142	
Carcinus maenas (L., 1758)	96 (74)	6-72 (6-68)	WW=16.12*Number lnWW= -7.785+2.836*lnCW (n=286, r^2=0.96)
Eriocheir sinensis H. Milne-Edwards, 1851	(11)	(46-70)	
Hemigrapsus penicillatus (de Haan, 1835)	1	20	
Hyas araneus (L., 1758)	4	33-49	
Liocarcinus arcuatus (Leach, 1814)	74	7-40	WW=1.50*Number
Liocarcinus depurator (L. 1758)	42	11-56	
Liocarcinus holsatus (Fabricius, 1798)	60 (16)	7-55 (7-51)	WW=9.45*Number lnWW= -6.835+2.538*lnCW (n=101, r^2=0.93)
Liocarcinus marmoreus (Leach, 1814)	(1)	(16)	
Necora puber (L., 1767)	4	22-68	
Macropodia rostrata (L., 1761)	60		WW=0.01*Number
Crustacea - Anomura (hermit crabs)			
Pagurus bernhardus (L., 1758)	85 (5)		WW=4.10*Number (incl. gastropod shell)
Pisidia longicornis (L., 1767)	2		
Crustacea - Astacidea (lobsters)			
Homarus gammarus (L., 1758)	4	115-220	
Mollusca - Cephalopoda (squids-cuttlefish)			
Loligo vulgaris Lamarck, 1798	6	ca. 100	
Sepia officinalis L., 1758	3	ca. 60	
Sepiola atlantica d'Orbigny, 1839	6	ca. 20	WW=0.03*Number

spring (Table 5.4). The total average density and biomass amounted to 3500 ind/1000m² and 1700 gADW/1000m². Catches were dominated by echinoderms (60%) and caridean shrimps (30%), followed by brachyuran crabs (9%), anomuran crabs (3%), caridean prawns (1%), and cephalopods (< 1%). Starfish *Asterias rubens*, brown shrimp *Crangon crangon* and shore crab *Carcinus maenas* were present in almost all samples, followed by hermit crab *Pagurus bernhardus*, brittlestars (*Ophiura* species) and arch-fronted swimming crab *Liocarcinus arcuatus* in >70% of the samples (Table 5.2). Five more species were found in > 30% of the samples, 3 in >10% and 18 species in <10% of the Oosterschelde samples.

In the Westerschelde, 8 macro-invertebrate species were recorded, of which 2 species (*Eriocheir sinensis* and *Liocarcinus marmoreus*) were not caught in the Oosterschelde. On average 3 species per sample were recorded with the lowest diversity in winter and in the eastern part (Table 5.5). The total average density and biomass amounted to 1600 ind/1000m² and 240 gADW/1000m², with an overall dominance of caridean shrimps (96%) followed by caridean prawns (2%), brachyuran crabs (1%) and hermit crabs (< 1%). *C. crangon* occurred in all samples, *C. maenas* and the prawn *Palaemon longirostris* in >40% of the samples, two more species in >10% and 3 in <10% of the Westerschelde samples (Table 5.2).

Table 5.3 Environmental variables, averaged per season (± standard deviation) over the period 1999-2001 for the whole system, per subarea or as a gradient, in the Oosterschelde (OS) and Westerschelde (WS). Sediment characteristics only measured in February 2000

Variable	System	stations / subarea	Winter	Spring	Summer	Autumn
Temperature (°C)	OS	all stations	6 ± 0.2	15 ± 1.4	20 ± 0.4	8 ± 1.2
	WS	all stations	6 ± 0.4	16 ± 1.3	20 ± 0.5	9 ± 0.8
Salinity (psu)	OS	all stations	31 ± 0.6	30 ± 0.9	32 ± 0.9	33 ± 1.4
	WS	gradient (stat2 to 14)	25 to 7	25 to 8	28 to 15	28 to 11
Dissolved oxygen ($mg.l^{-1}$)	OS	all stations	10 ± 0.2	10 ± 1.8	7 ± 0.3	9 ± 0.3
	WS	Western	10 ± 0.2	10 ± 0.9	6 ± 0.5	9 ± 0.6
		Eastern	9 ± 0.6	7 ± 1.5	6 ± 0.3	9 ± 1.3
Turbidity (m^{-1})	OS	Western-Central	0.7 ± 0.4	0.3 ± 0.1	0.4 ± 0.1	0.6 ± 0.2
		Eastern-Northern	0.4 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.04
	WS	Western	1.7 ± 0.2	1.1 ± 0.3	1.6 ± 0.6	2.1 ± 0.4
		Eastern	2.4 ± 1.1	2.0 ± 0.5	1.4 ± 0.3	2.3 ± 0.6
Median grainsize (µm)	OS	Western	218 ± 21 (except stat10: 89)			
		Central	164 ± 21			
		Eastern	188 ± 51			
		Northern	45 ± 14			
	WS	gradient (stat2 to 14)	430 to 230			
Silt concentration (%)	OS	Western	10 ± 2 (except stat10: 39)			
		Central	6 ± 1 (stat17 & 26); 26 ± 11 (stat21 & 24)			
		Eastern	9 ± 5			
		Northern	57 ± 7			
	WS	all stations	0 (except stat4: 2)			

5.3.2 Environmental variables

The temperature regime was comparable in both systems and mainly varied seasonally, with winter minima (6°C) and summer maxima (20°C). The largest differences between the succeeding years were recorded in spring and autumn (Table 5.3). In the Oosterschelde temperature increased in spring and decreased in autumn with 2°C from the western to the eastern stations. In the Westerschelde a small increase from west to east was noted during every season. Salinity stayed the same throughout the Oosterschelde with values around 30 psu in spring and 33 psu in autumn. In the Westerschelde salinity decreased from west to east: from 25 to 7 psu in winter and spring, and from 28 to 11 psu in summer and autumn. Except for spring, the dissolved oxygen concentration remained more or less the same per season in both systems, with summer minima (7 and 6 $mg.l^{-1}$) and winter maxima (10 and 9 $mg.l^{-1}$) respectively in the Oosterschelde and the Westerschelde. In spring the oxygen concentration dropped from 10 $mg.l^{-1}$ in the western part to 7 $mg.l^{-1}$ in the eastern part of the Westerschelde, although the variation between the succeeding years was largest in spring in both systems. In the western and central parts of the Oosterschelde turbidity was highest in winter and autumn (0.6 to 0.7 m^{-1}), while in the eastern and northern parts turbidity was 0.3 to 0.4 m^{-1}. In the Westerschelde turbidity was much higher, with higher values in the eastern part for most seasons (>2 m^{-1}). The median grain size was >200 µm in the western part of the Oosterschelde (except at station 10), and on average 164 µm in the eastern and central parts. At most stations in these subareas less than 10% silt was noted, except at stations 10, 21 and 24. In the northern part the median grain size was on average 45 µm and the silt fraction amounted to 50-64%. In the Westerschelde the sediment was coarser, with a decreasing median grain size from 430 µm in the western to 230 µm in the eastern part, and only at station 4 a small percentage of silt (2%) was noted.

5.3.3 Community analyses

Canonical Correspondence Analysis (CCA, based on 32 species) of the Oosterschelde data, clearly showed a seasonal separation along the first ordination axis. This was related to temperature and dissolved oxygen concentration (Fig.5.2). Most prawn and shrimp species were located in the winter-autumn quadrants, while cephalopods seemed to be correlated with summer. Both sampling years for spring where divided along the second axis, with most brachyuran and anomuran crabs and echinoderms located near the centre of the plot. Total inertia amounted to 1.6; only 6.4% of the variance could be explained. No clear spatial separation was noted although most western stations were located near the higher turbidity-salinity reaches along the second axis. Most northern and eastern stations were found near each other per season, except for spring.

The CCA (based on 8 species) for the Westerschelde showed a spatial separation between the western and eastern stations along the first axis, correlated with salinity and turbidity. *Palaemon longirostris* and *Eriocheir sinsensis* were typical species for the eastern part. A seasonal separation (correlated with dissolved oxygen concentration and temperature) was clearly visible along the second axis, with *Carcinus maenas* as typical species for the warmer months, *Liocarcinus holsatus* for summer, and *Pan-*

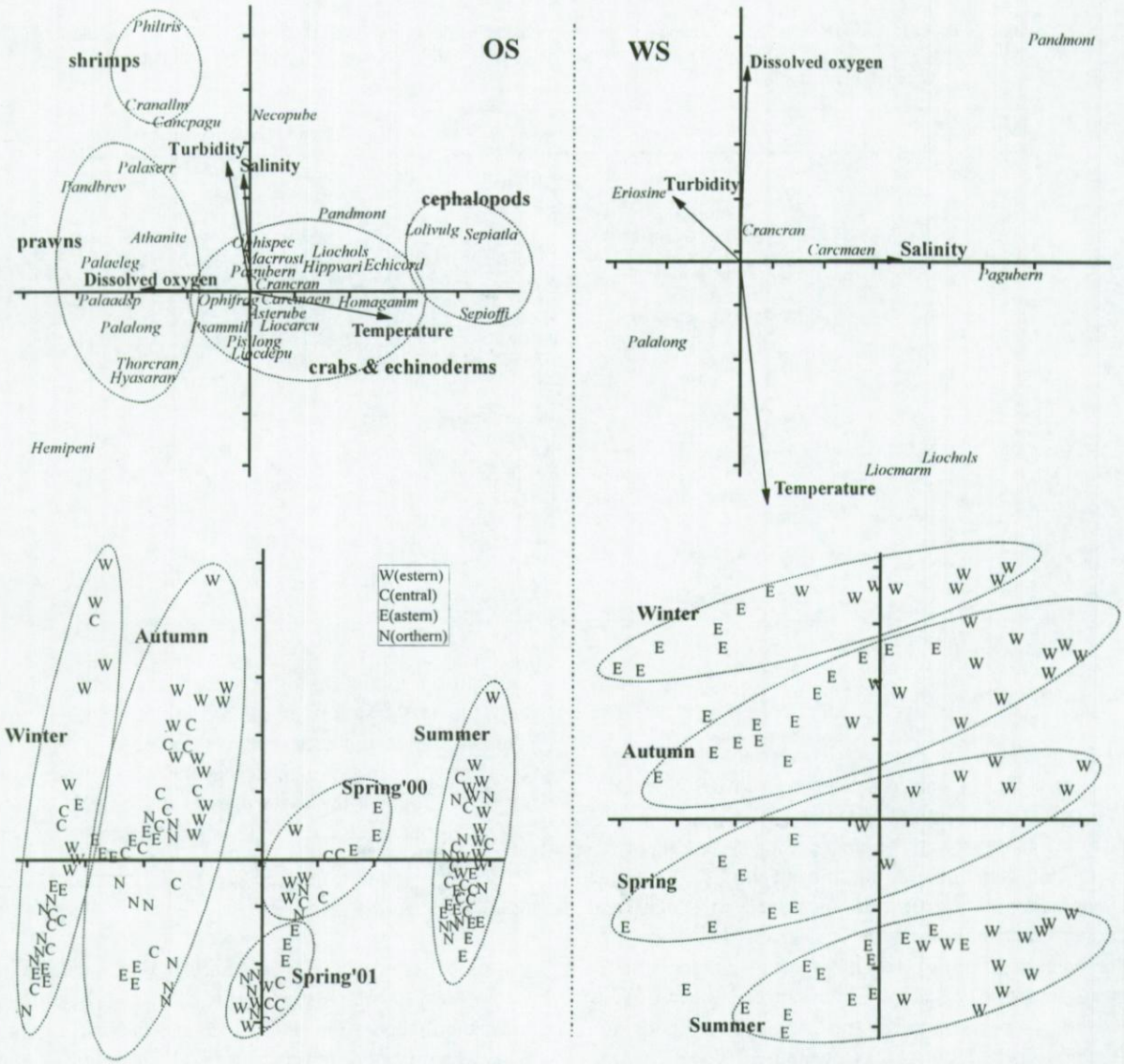

Fig.5.2 Species-environmental biplots and sample plots as the results of the Canonical Correspondence Analyses with the Oosterschelde (OS) and Westerschelde (WS) data in the plane of the first two ordination axes

dalus montagui for autumn in the western part. Total inertia amounted to 0.8; 22% of the variance could be explained.

5.3.4 Spatial and temporal patterns in density, biomass and growth

The length ranges per species are given in Table 5.2. The average density and biomass per season and per subarea for all macro-invertebrate species is given in Table 5.4 for the Oosterschelde and in Table 5.5 for the Westerschelde for the period 1999-2001, and in Table 5.6 for 4 species for the period 1988-89. The values in the latter table may differ from the ones given in the introduction, as a shorter period has been taken into account for this study. The length-frequency distributions for the period 1999-2001 in both systems are shown in Fig.5.3 for the commonest species (per season and per sex), and in Fig.5.4 for the caridean prawns (averaged per species).

Echinoderms

Six echinoderms were recorded in the Oosterschelde, while none were recorded from the Westerschelde. Starfish *Asterias rubens* showed highest densities and biomasses in the northern and western parts, which were three times higher than in the central part and six times higher than in the eastern part. On average 400 ind/1000m² and 800 gADW/1000m² were recorded over the whole period, with an increase from winter to summer and a slight decrease towards autumn. Most length classes (range 5 - 165 mm) were present throughout the year, although a high input of new recruits was seen in summer (modal length 20-30 mm) with a clear growth increase towards winter (modal length 70 mm). The total average density and biomass for the whole subtidal area (220 km²) amounted to 9 10^7 individuals and 185 tonnes ADW in 1999-2001. In comparison with the period 1988-

Table 5.4 Average density, species richness and average biomass per subarea and season for the period 1999-2001 in the Oosterschelde

	Winter				Spring				Summer				Autumn			
Density (#/1000m²)	Western	Central	Eastern	Northern	Western	Central	Eastern	Northern	Western	Central	Eastern	Northern	Western	Central	Eastern	Northern
Asterias rubens	360	55	60	745	505	250	85	550	940	255	185	530	620	275	50	785
Ophiothrix fragilis	0.2	1	150	30	2	10	10	75	45	-	30	40	15	153	15	60
Ophiura ophiura & O. albida	6800	175	50	95	11500	135	75	170	2165	110	2	105	3315	290	65	20
Echinocardium cordatum	1	-	-	-	25	2	1	1	10	0.3	-	1	0.2	-	-	-
Psammechinus miliaris	20	5	0.3	10	10	10	0.3	30	5	-	-	10	5	5	-	15
Crangon allmanni	0.2	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-
Crangon crangon	400	285	5625	370	585	665	175	305	2045	1250	620	1505	370	1410	905	415
Philocheras trispinosus	5	0.5	-	-	-	-	-	-	-	-	-	-	2	0.2	-	-
Athanas nitescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-
Hippolyte varians	-	-	1	-	-	-	1	-	-	-	5	-	0.5	-	-	-
Palaemon adspersus	-	-	250	-	-	-	-	-	-	-	-	-	-	0.2	160	0.5
Palaemon elegans	-	0.2	5	-	-	-	-	-	-	-	-	-	-	0.5	15	-
Palaemon longirostris	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Palaemon serratus	2	0.5	1	-	-	-	-	-	-	-	-	-	1	10	1	5
Pandalina brevirostris	0.5	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	0.2
Pandalus montagui	1	-	-	-	-	0.2	-	-	25	5	5	1	5	5	-	0.5
Thoralus cranchii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
Cancer pagurus	-	-	-	-	-	-	-	-	-	-	-	-	0.2	0.5	-	-
Carcinus maenas	55	15	140	145	220	115	215	665	210	60	135	295	200	90	110	90
Hemigrapsus penicillatus	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyas araneus	-	0.2	0.5	-	-	0.2	-	-	-	-	-	-	-	0.5	-	-
Liocarcinus arcuatus	2	10	95	85	40	30	45	70	70	25	70	155	5	75	50	85
Liocarcinus depurator	5	1	1	170	5	10	1	120	10	-	-	220	2	20	5	120
Liocarcinus holsatus	5	0.2	-	10	35	2	2	20	205	15	1	120	45	5	0.5	20
Necora puber	0.2	-	-	-	-	-	-	-	-	-	-	2	0.5	-	-	-
Macropodia rostrata	20	2	5	5	15	1	1	-	25	10	45	20	20	10	10	10
Pagurus bernhardus	280	75	25	120	315	190	25	85	245	90	10	55	140	60	15	25
Pisidia longicornis	-	-	-	0.5	-	-	-	-	-	-	-	1	-	1	-	-
Homarus gammarus	-	-	-	-	-	-	-	-	-	0.5	-	0.2	-	0.5	-	-
Loligo vulgaris	-	-	-	-	-	-	-	-	0.5	2	-	1	0.2	-	0.2	-
Sepia officinalis	-	-	-	-	-	-	-	-	1	1	5	-	-	-	-	-
Sepiola atlantica	-	-	-	-	-	0.2	-	-	5	2	-	5	-	-	-	-
Total Density	7950	630	6400	1785	13260	1415	640	2100	6000	1830	1115	3055	4745	2275	1400	1640
Number of species	18	17	15	13	12	15	13	11	16	14	12	18	20	20	16	16
Biomass (gADW/1000m²)																
Asterias rubens	720	110	120	1480	1010	500	170	1095	1865	505	365	1055	1235	600	95	1560
Ophiothrix fragilis	0.05	0.2	25	5	0.5	1	2	10	10	-	5	5	2	2	5	10
Ophiura ophiura & O. albida	855	20	10	10	780	15	5	15	155	10	0.1	10	285	25	10	1
Echinocardium cordatum	10	-	-	-	190	15	5	10	60	2	-	10	1	-	-	-
Psammechinus miliaris	65	10	1	35	25	30	1	100	15	-	-	35	15	20	-	45
Crangon allmanni	0.01	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-
Crangon crangon	50	35	655	45	70	80	20	35	240	145	75	175	45	165	105	50
Philocheras trispinosus	0.05	0.002	-	-	-	-	-	-	-	-	-	-	0.01	0.001	-	-
Athanas nitescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-
Hippolyte varians	-	-	0.1	-	-	-	0.1	-	-	-	0.5	-	0.05	-	-	-
Palaemon adspersus	-	-	30	-	-	-	-	-	-	-	-	-	-	0.02	20	0.05
Palaemon elegans	-	0.05	1	-	-	-	-	-	-	-	-	-	-	0.1	2	-
Palaemon longirostris	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	0.1	-
Palaemon serratus	0.2	0.05	0.1	-	-	-	-	-	-	-	-	-	0.1	1	0.1	0.5
Pandalina brevirostris	0.1	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	0.02
Pandalus montagui	0.1	-	-	-	-	0.05	-	-	5	1	0.5	0.1	0.5	1	-	0.05
Thoralus cranchii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Cancer pagurus	-	-	-	-	-	-	-	-	-	-	-	-	5	20	-	-
Carcinus maenas	135	30	340	330	540	275	520	1610	495	150	330	715	485	240	225	215
Hemigrapsus penicillatus	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyas araneus	-	1	1	-	-	1	-	-	-	65	-	5	-	30	-	-
Liocarcinus arcuatus	-	5	25	25	10	10	15	20	20	5	15	40	2	25	20	20
Liocarcinus depurator	10	2	1	240	5	15	1	175	20	-	-	310	5	30	5	170
Liocarcinus holsatus	5	0.5	-	15	50	5	5	30	290	20	1	165	60	10	1	25
Necora puber	0.5	-	-	-	-	-	-	-	-	-	-	5	1	-	-	-
Macropodia rostrata	0.05	0.005	0.01	0.01	0.05	0.001	0.002	-	0.05	0.02	0.1	0.05	0.05	0.02	0.02	0.02
Pagurus bernhardus	170	50	15	75	195	120	15	50	150	55	10	35	90	40	10	15
Pisidia longicornis	-	-	-	0.1	-	-	-	-	-	-	-	0.2	-	0.5	-	-
Homarus gammarus	-	-	-	-	-	-	-	-	-	65	-	5	-	25	-	-
Loligo vulgaris	-	-	-	-	-	-	-	-	1	10	-	10	2	-	10	-
Sepia officinalis	-	-	-	-	-	-	-	-	0.01	0.01	0.05	-	-	-	-	-
Sepiola atlantica	-	-	-	-	-	0.002	-	-	0.05	0.01	-	0.02	-	-	-	-
Total Biomass	2010	260	1220	2255	2870	1050	755	3155	3315	1030	795	2570	2220	1230	500	2105

89, starfish densities almost doubled in the western and central parts in 1999-2001, but decreased with 65% in the eastern part. This could be attributed to an exceptionally high value of 5600 ind/1000m² in summer 1989 at station 33. Also, the autumn averages were much lower during 1988-89.

Three ophiuroid species were found in the Oosterschelde throughout the year. Some *Ophiura* subsamples were analysed and 2 species were deter-

mined: *Ophiura ophiura* and *Ophiura albida*. Together they were very abundant (on average 3400 ind/1000m² in spring), although the high values were mainly recorded in the western part (on average 5300 ind/1000m², with a peak of 73000 ind/1000m² at station 10 in May 2000). In the other subareas the average density varied between 45 and 180 ind/1000m².

Judging from the number/weight ratio and the determined subsamples, the larger *O. ophiura* seemed to be more abundant in 2001, while during summer and autumn both *Ophiura* species (mainly juveniles) seemed to be equally abundant. On the contrary, the less common brittlestar *Ophiotrix fragilis* (on average 40 ind/1000m² in winter) was preferably found in the eastern and northern parts with a peak density of 460 ind/1000m² at station 38 in No-

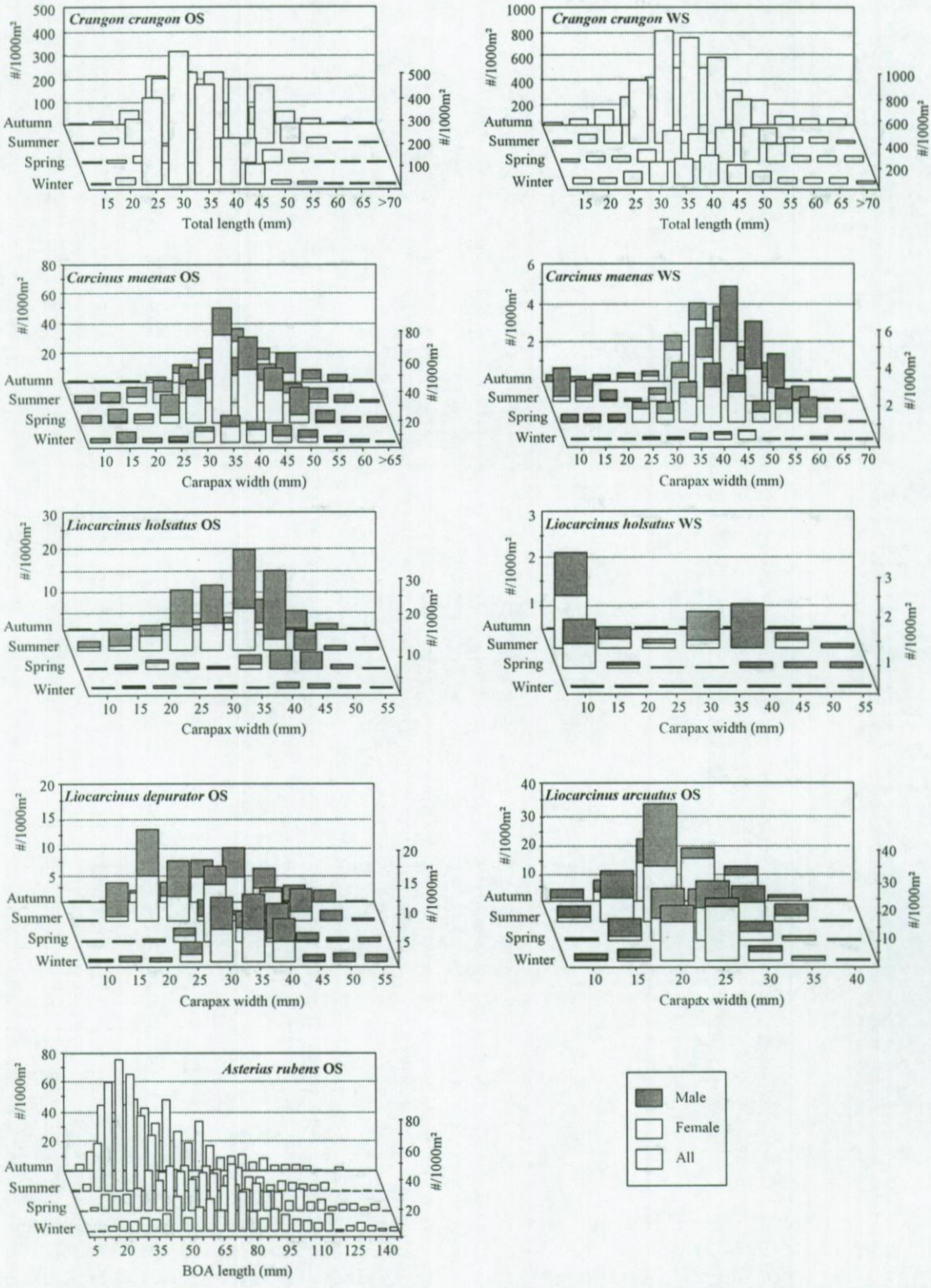

Fig.5.3 Length-frequency distributions divided per season (and per sexe) for the most relevant species in the Oosterschelde (OS) and Westerschelde (WS). Note the different scales and measurements

vember 2000. For the three ophiuroids together the total average biomass amounted to 160 gADW/1000m², while for most subareas (except the western part) the average biomass oscillated around 15 gADW/1000m². Calculated for the whole subtidal area this led to 4 10^8 ophiuroids with a total weight of 36 tonnes ADW. No data on ophiuroids were available for the period 1988-89.

The echinoids were represented by 2 species in the Oosterschelde. The common sea-urchin *Psammechinus miliaris* was present throughout the year (on average 7 ind/1000m²), with higher densities in spring and winter. Sea-urchins preferred the northern and western parts and were almost absent from the eastern part. The heart-urchin *Echinocardium cordatum* was less common and mainly present in the western part in spring (8 ind/1000m²) and summer. The total average biomass for the period 1999-2001 amounted to 20 gADW/1000m² for each of the 2 echinoids, which could be converted to 9 tonnes ADW or 2 10^6 echinoids in the whole subtidal Oosterschelde. Also for the echinoids no data were available for the period 1988-89.

Caridean shrimps

The caridean shrimps were represented by 3 species in the Oosterschelde and only 1 species in the Westerschelde. Brown shrimp *Crangon crangon* was the overall dominating shrimp species in both systems throughout the year, with a population increase towards an average summer maximum of 1400 and 2900 ind/1000m² (160 and 320 gADW/1000m²) in the Oosterschelde and Westerschelde, respectively. Although, the maxima were located in different subareas per season in the Oosterschelde, the average densities were comparable for most subareas (<1000 ind/1000m²), except for the eastern part with a peak density of 18700 ind/1000m² at station 33 in February 2000. In the Westerschelde the average densities and biomasses were twice as high in the eastern part for most seasons, except in spring with an average density three times higher in the western part. All length classes (15-75 mm TL) were found throughout the year, with a continuous input of small individuals (<25 mm) in both systems. The modal length-class was 30-35 mm TL in all seasons for the Oosterschelde, while in the Westerschelde an increase in modal length was noted from 35 mm in summer to 45 mm in spring. In comparison with the period 1988-89, the average density and biomass of *C. crangon* showed a large increase in all subareas of the Oosterschelde during all seasons of 1999-2001. For the whole subtidal Oosterschelde this amounted to 2 10^8 individuals and 28 tonnes ADW. In contrast, the average density of brown shrimp decreased with 50% in the western part and with 35% in the eastern part of the Westerschelde, which was mainly visible in summer and autumn. This led to total averaged values for the subtidal population of 3 10^8 individuals and 38 tonnes ADW.

The similar species *Crangon allmanni* was recorded a few times in the western part of the Oosterschelde in February 2000 and November 2001. Also, *Philocheras trispinosus* was only found in autumn and winter in the Oosterschelde with an average density of 1.3 ind/1000m² in the western part. The length range of the latter species varied between 13 and 25 mm TL.

Caridean prawns

In the Oosterschelde 9 caridean prawns were recorded. Most prawns occurred in autumn and winter, except *Hippolyte varians* and *Pandalus montagui,* which were found throughout the year with higher densities in summer. Five prawn species were typically found in the eastern part, where *Palaemon adspersus* was the commonest species (on average 100 ind/1000m²) followed by *Palaemon elegans* at much lower densities. *Athanas nitescens* was only caught once and *Palaemon longirostris* a few times in the eastern part of the Oosterschelde. *P. montagui* and *Palaemon serratus* were more common throughout the Oosterschelde with a preference for the western and central part, respectively. *Pandalina brevirostris* was recorded a few times during one winter and a single record of *Thoralus cranchii* was made in the northern part. The length ranges were successive with *A. nitescens*, *T. cranchii, H. varians* and *P. brevirostris* being the smallest (20-40 mm TL), followed by 4 other species (modal length classes 35, 45 and 50 mm) and *P. serratus* being the largest (up to 90 mm). The averaged subtidal density and biomass of all prawns together amounted to 6 10^6 individuals or 1 tonnes ADW.

In the Westerschelde only 2 prawn species were found: *Palaemon longirostris* in the eastern part

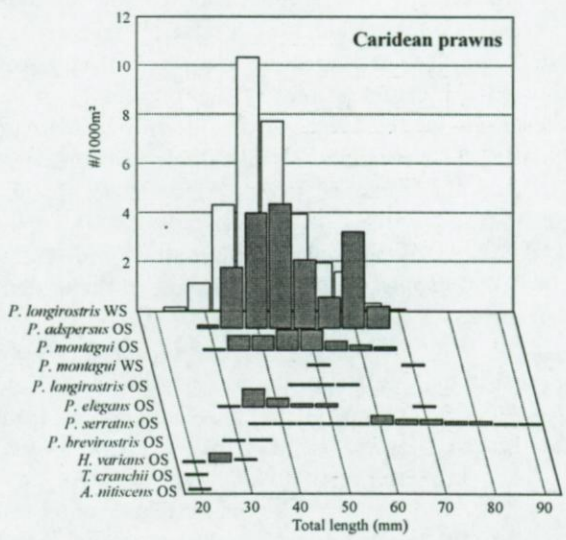

Fig.5.4 Length-frequency distributions for 9 prawn species in the Oosterschelde (OS) and 2 prawn species in the Westerschelde (WS)

(on average 70 ind/1000m²) and *Pandalus montagui* in the western part (<1 ind/1000m²). The average density of *P. longirostris* increased from spring to summer, while the species was almost absent in winter. Individuals between 25 and 67 mm TL were caught, with a modal length class of 40-45 mm. The subtidal density and biomass of *P. longirostris* equalled the values of all prawns together in the Oosterschelde. No comparison for caridean prawns was possible with the period 1988-89.

Brachyuran crabs

In total 11 crab species were recorded during 1999-2001, of which 9 species in the Oosterschelde and 4 species in the Westerschelde. In both systems shore crab *Carcinus maenas* was the most abundant species throughout the year, with decreasing densities from spring to winter. In the Oosterschelde the average density and biomass were highest in the northern part (280 ind/1000m² and 670 gADW/1000m²); 35 to 50% lower in the western and eastern part and lowest in the central part. In the Westerschelde densities were much lower than in the Oosterschelde. The average density was twice higher in the western part (20 ind/1000m²), except during summer when the population of *C. maenas* was more or less evenly distributed throughout the Westerschelde. A small input of new recruits (10-15 mm CW) could be seen in spring and summer; while the commonest length classes (35-45 mm) were present throughout the year. The sex ratio was comparable in both systems with a little bit more females than males. Gravid females were mainly found in spring, when 20 and 30% of the females bore eggs in the Oosterschelde and Westerschelde, respectively. The infection rate with *Sacculina carcini* was equal between both sexes, but much higher in the Oosterschelde (on average 30%) in comparison with the Westerschelde (< 2%). Apparently, the infection rate was highest in the northern and eastern part of the Oosterschelde. In comparison with the period 1988-89, the average density doubled in the Oosterschelde in 1999-2001 and even showed a fourfold increase in spring, while in the Westerschelde the average densities only increased a little bit. This resulted in total subtidal averages of 4 10^7 individuals and 88 tonnes ADW in the Oosterschelde and only 3 10^6 individuals or 10 tonnes ADW in the Westerschelde. In contrast with 1999-2001, *C. maenas* was more abundant in the eastern part in 1988-89.

Three species of the genus *Liocarcinus* were present in the Oosterschelde. It is worthwhile to note that d'Udekem d'Acoz (1999) placed all species from the genera *Liocarcinus, Necora, Macropipus* and *Polybius* into one monophyletic genus named *Polybius*. Until more clarity is given on this taxonomical problem, we preferred to keep the more established names given in Adema (1991a). Arch-fronted swimming crab *Liocarcinus arcuatus* was the most abundant species (on average 60 ind/1000m²), but harbour crab *Liocarcinus depurator* and flying crab *Liocarcinus holsatus* showed the highest average biomass (both 50 gADW/1000m²). Most length classes of the three species were present during all seasons throughout the Oosterschelde with higher densities towards summer. *L. arcuatus* is a small species (modal length class 20-25 mm CW) with highest densities in the northern part (100 ind/1000m²) and 2 or 3 times lower densities in the other subareas. In spring and summer males constituted 55% of the population, while in autumn and winter around 70% were females. *L. depurator* was almost exclusively present in the northern part (on average 160 ind/1000m²). *L. holsatus* was a typical summer species with highest average densities in the western part of the Oosterschelde (90 ind/1000m²) and a peak of 1240 ind/1000m² at station 5 in August 2001. In the Westerschelde *L. holsatus* occurred at low densities, mainly in the western part in summer (on average 7 ind/1000m²) and in spring. The highest number of new recruits (< 15 mm) of *L. depurator* and *L. holsatus* (modal length class 30-40 mm) was found in summer. In the Oosterschelde on average 56% of *L. depurator* were males, but for *L. holsatus* at least twice as many males as females were found during every season. On average 70% of these males had a carapace width >30 mm. Also, in the Westerschelde twice as many males were present. In spring almost all females of *L. depurator* bore eggs, while no gravid females were noted for *L. holsatus*. Almost no swimming crabs were infected with *Sacculina carcini* in both systems. In comparison with the period 1988-89 the average densities of *L. holsatus* in the Oosterschelde increased substantially in summer and autumn, mainly in the western (and northern) part, but the species almost disappeared from the eastern part in 1999-2001. In the Westerschelde the average densities were halved during the latter period. For the whole subtidal Oosterschelde this meant 3 10^7 individuals or 32 tonnes ADW, while for the Westerschelde the subtidal averages only amounted to 4 10^5 individuals of *L. holsatus* (= 1 tonnes ADW).

Five more crab species were recorded in the Oosterschelde: edible crab *Cancer pagurus*, velvet swimming crab *Necora puber*, japanese crab *Hemigrapsus penicillatus*, great spider crab *Hyas araneus* and long legged spider crab *Macropodia rostrata*. *C. pagurus* was only caught a few times in autumn. *N. puber* was mainly caught in summer in the western and northern part (average density 0.2 ind/1000m²). *H. penicillatus* was caught once in February 2001. *H. araneus* was not caught in summer, and reached an average density of 0.1 ind/1000m² during the other seasons in the central and eastern part. *M. rostrata* was more common throughout the Oosterschelde with highest densities in summer and autumn (respectively 25 and 13 ind/1000m²).

Table 5.5 Average density, species richness and average biomass per subarea and season for the period 1999-2001 in the Westerschelde

	Winter		Spring		Summer		Autumn	
	Western	Eastern	Western	Eastern	Western	Eastern	Western	Eastern
Density (#/1000m²)								
Crangon crangon	450	900	1425	505	1830	3900	840	2465
Palaemon longirostris	-	0.5	1	80	-	135	2	40
Pandalus montagui	-	-	0.2	-	-	-	0.5	-
Carcinus maenas	3	-	25	10	30	20	20	10
Eriocheir sinensis	0.5	-	-	1	-	0.2	-	1
Liocarcinus holsatus	-	-	5	-	10	5	-	-
Liocarcinus marmoreus	-	-	-	-	0.2	-	-	-
Pagurus bernhardus	-	-	0.5	-	0.5	-	0.5	-
Total density	455	900	1450	590	1865	4060	865	2510
Number of species	3	2	6	4	5	5	5	4
Biomass (gADW/1000m²)								
Crangon crangon	55	80	240	55	225	410	130	310
Palaemon longirostris	-	0.05	0.1	5	-	10	0.2	5
Pandalus montagui	-	-	0.1	-	-	-	-	-
Carcinus maenas	10	-	95	15	110	60	80	15
Eriocheir sinensis	2	-	-	10	-	0.5	-	5
Liocarcinus holsatus	-	-	2	-	10	0.5	-	-
Liocarcinus marmoreus	-	-	-	-	-	-	-	-
Pagurus bernhardus	-	-	0.3	-	0.2	-	0.2	-
Total biomass	65	80	340	80	340	485	210	335

Table 5.6 Average density and biomass of 4 species per subarea and season for the period 1988-89 in the Oosterschelde and Westerschelde

		Density (#/1000m²)				Biomass (gADW/1000m²)			
		Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Oosterschelde									
Asterias rubens	Western	120	320	630	50	235	640	1250	95
	Central	140	365	55	20	275	730	110	45
	Eastern	50	105	1010	85	100	205	2010	170
	Northern	175	2940	70	420	350	5850	140	840
Crangon crangon	Western	190	710	985	360	20	85	115	45
	Central	205	220	315	60	25	25	40	10
	Eastern	415	15	30	90	50	2	5	10
	Northern	30	20	735	190	5	2	85	20
Carcinus maenas	Western	5	45	20	60	15	105	50	145
	Central	5	40	20	10	10	100	45	15
	Eastern	175	110	250	35	425	260	600	90
	Northern	10	35	20	20	20	90	45	50
Liocarcinus holsatus	Western	10	10	35	15	15	20	50	20
	Central	0.5	5	20	2	1	10	25	5
	Eastern	0.5	2	5	2	0.5	2	10	5
	Northern	1	60	25	10	1	85	35	10
Westerschelde									
Crangon crangon	Western	695	1670	3910	2435	105	255	590	370
	Eastern	580	900	6275	5985	90	140	950	905
Carcinus maenas	Western	1	25	25	20	2	85	80	60
	Eastern	-	15	15	5	-	15	45	10
Liocarcinus holsatus	Western	-	10	20	2	-	10	25	5
	Eastern	-	-	0.5	-	-	-	1	-

Two crab species were recorded in the Westerschelde only: marbled swimming crab *Liocarcinus marmoreus* (one record in August 1999) and Chinese mitten crab *Eriocheir sinensis*. The latter species was mainly found in the eastern part at low densities throughout the year (average 0.5 ind/1000m²).

Anomuran crabs

Two anomuran species were noted in the Oosterschelde. Hermit crab *Pagurus bernhardus* was very common during the whole period (on average 110 ind/1000m² and 70 gADW/1000m² including the gastropod shells), with lowest densities in autumn. The highest densities were recorded in the western part, while the species was less common in the eastern part. Porcelain crab *Pisidia longicornis* was caught a few times in the central and northern part of the Oosterschelde, but not during spring. *P. bernhardus* was also caught a few times in the western part of the Westerschelde (average density 0.3 ind/1000m²), but was completely absent during winter. For the whole subtidal Oosterschelde an averaged density of 3 10^7 individuals was calculated. No comparison could be made for the anomuran crabs with the period 1988-89.

Lobsters

Juvenile lobster *Homarus gammarus* was caught a few times in summer and autumn in the central part of the Oosterschelde, with a length varying between 115 and 220 mm TL. No lobsters were recorded from the Westerschelde.

Cephalopods

No cephalopods were found in the Westerschelde an no comparison could be made with the period 1988-89. In the Oosterschelde 3 species were recorded sporadically at several stations: common squid *Loligo vulgaris*, common cuttlefish *Sepia officinalis* and little cuttlefish *Sepiola atlantica*. All species mainly occurred in summer at low densities (on average 1, 2 and 3 ind/1000m² respectively). Only the juveniles of *L. vulgaris* and *S. officinalis* were caught. They were found throughout the Oosterschelde, but *L. vulgaris* mainly in the central part, *S. officinalis* in the eastern part and *S. atlantica* in the western part. If converted for the subtidal area approximately 4 10^5 cephalopods were present in the Oosterschelde during the period 1999-2001.

5.4 Discussion

5.4.1 Abiotic influences on the macro-invertebrate diversity

The large difference in species richness between the Oosterschelde (33 species) and the Westerschelde (8 species) could partly be attributed to the fact that only few species can withstand the harsh estuarine conditions (*e.g* the large salinity fluctuations and much higher turbidities) in the Westerschelde. The absence of heart-urchin *Echinocardium cordatum* from the Westerschelde could probably be related with the high turbidity values, as it was shown that the occurrence of this species was only partly related with sediment type and higher salinity preferences (Wolff 1968). The distribution of common cuttlefish *Sepia officinalis* (and probably also the other cephalopods) was limited by salinity in most parts of the Delta area (Paulij *et al.* 1990). In the Oosterschelde low densities of *Sepiola atlantica* were recorded, comparable with an average density of 2 ind/1000m² in Firemore Bay (Scotland) (Yau & Boyle 1996).

Low salinities in the Westerschelde deterred most marine offshore species. The Oosterschelde was altered from a real estuary into a marine bay, which probably explained why marine offshore species entered the system more frequently. The caridean shrimps *Crangon allmanni* and *Philocheras trispinosus* are typical inhabitants of sublittoral offshore areas along the European coasts (Allen 1960, Oh & Hartnoll 1999). Both species more or less replaced *Crangon crangon* on the offshore (Hinder) sandbanks of the Belgian Continental Shelf (Oyugi 1999). Also, marbled swimming crab *Liocarcinus marmoreus*, caught once in summer in the mouth of the Westerschelde, could be classified as a wandering offshore individual (Adema 1991a). The loss of a salinity gradient in the Oosterschelde influenced the colouring of shore crab *Carcinus maenas*. This can vary from green to red, respectively related to the beginning and the end period of the intermoulting stage, but also related to their tolerance of salinity fluctuations (Reid *et al.* 1997). In the Westerschelde more green individuals were caught, while in the Oosterschelde more individuals were reddish. Also, in the UK *C. maenas* was shown to be predominantly green in the estuaries, while red and orange crabs were more abundant on the open shore (McGaw & Naylor 1992).

Although, the diversity in the Oosterschelde amounted to 33 species in 1999-2001, several species were only sporadically caught, related with their sediment/habitat preferences. Both long-legged spider crab *Macropodia rostrata* and brittlestar *Ophiothrix fragilis* prefer strong currents and a rough substrate (Wolff 1968, Wolff & Sandee 1971). Compared to the latter study *M. rostrata* was better represented in 1999-2001 in the Oosterschelde. Several prawn species were frequently seen by divers in the Oosterschelde, either between algae and sponges (*e.g Hippolyte varians*) or in stone crevices (*e.g Thoralus cranchii* and *Athanas nitescens*). Before 1994, the latter species was never recorded in the Oosterschelde (www.anemoon.org). The caridean prawn *Pandalina brevirostris* often occurs on coarse shell-

gravel (Smaldon *et al.* 1993). In the German Bight juveniles of *P. brevirostris* were exclusively collected from estuarine habitats (Wehrtmann & Greve 1995), but this species was not recorded from the Oosterschelde before the 1980s (Heerebout 1974). Porcelain crab *Pisidia longicornis* seemed to be common intertidally in the Delta area, while great spider crab *Hyas araneus* was confined to rough bottoms such like stones or oysterbeds (Wolff & Sandee 1971). The latter species was more common in the central and eastern part of the Oosterschelde, while in the Forth (UK) the number of *H. araneus* increased towards the mouth of the estuary (Mathieson & Berry 1997).

It was remarkable that *Palaemon adspersus* was the commonest prawn species in the Oosterschelde, because till the 1980s this species was almost not caught in the Dutch Delta area (Adema 1988). *P. adspersus* mostly occurred in marine bays in *Zostera* beds and between macro-algae (Pihl 1986, d'Udekem d'Acoz 1999). After the building of the storm-surge barrier only few *Zostera* beds were left in the Oosterschelde, mainly around the transition zone between the central and eastern part (van Berchum & Wattel 1997). Perhaps, *P. adspersus* could also profit of the presence of one type of green algae (*Vaucheria* species) in the eastern part. On the other hand, *Palaemon elegans* used to be quite common in the polyhaline parts during the 1960s (Heerebout 1974), while in 1999-2001 it was almost exclusively caught in the eastern part of the Oosterschelde, probably related to the absence of eelgrass in the western part.

Another infrequent species during autumn in the Oosterschelde was edible crab *Cancer pagurus*. The distribution of this species was governed by temperature, in combination with the presence of hard substrate (Wolff & Sandee 1971). Temperature also influenced the presence of other macro-invertebrate species. For example, velvet swimming crab *Necora puber* disappeared from the Dutch delta area between 1985 and 1988, due to the strong winters of 1985 and 1986 (Adema 1991a). Experiments proved that larvae of *N. puber* could not tolerate low salinities and low temperatures (Choy 1991). Grey swimming crab *Liocarcinus vernalis* appeared in the Delta area from 1990 onwards. It was recorded in the ebb-tidal delta of the Grevelingen (part of the Voordelta) during several surveys in 1993-'94 (Hostens, unpubl. data). However, this species was not recorded from the Oosterschelde during 1999-2001 as it seemed to have disappeared again from the Dutch Delta after the cold winter of 1996 (Rappé & d'Udekem-d'Acoz 1997). Previously, the entire population of common sea-urchin *Psammechinus miliaris* had been destroyed by severe winters (Wolff 1968), while during the period 1999-2001 it was fairly common throughout the year in the Oosterschelde.

The effect of the different sources of both organic and inorganic pollutants in the Westerschelde on the biodiversity of mobile macro-invertebrates remained unclear. High densities of only a few and smaller species (cfr. the Westerschelde) are typical for polluted areas (Warwick & Clarke 1994). It was shown that the substantial concentrations of several pollutants at the end of the 1980s remained constant during the 1990s (Stronkhorst 1993, Baeyens 1998). In the beginning of the 1980s, between 10 and 50% of the *Carcinus maenas* population in the Oosterschelde was infected with the crustacean parasite *Sacculina carcini* (Adema 1991a). Throughout the whole period 1999-2001 the infection rate was high in the Oosterschelde, comparable with the Forth estuary (UK) (Mathieson *et al.* 1998), but almost nil in the Westerschelde. In Jacksonville (Florida, USA) it was shown that the absence of crustacean parasites on fish was associated with high pesticide levels and a mixture of metal and organic contaminants in combination with low salinity (Landsberg *et al.* 1998). This probably also explains the absence of *S. carcini* on *C. maenas* in the Westerschelde.

5.4.2 Biotic influences on the macro-invertebrate diversity

According to Adema (1991b) the crustacean diversity kept on increasing in the Delta area during the last decades of the 20th century. All estuarine and marine communities harbour so-called aliens, which have extended their natural range as a consequence of anthropogenic transportations (Little 2000). In the upper part of the Schelde estuary (the Lower Zeeschelde) 3 out of the 4 recorded crab species were exotics (Maes *et al.* 1998a). In the present study, Chinese mittencrab *Eriocheir sinensis* was only caught in the Westerschelde. This fairly large freshwater crab has to return at sea for breeding (d'Udekem d'Acoz 1999). This could explain why *E. sinensis* was not recorded from the saline water of the Oosterschelde, where the freshwater connections were closed off. The Delta works also had consequences for lobster *Homarus gammarus*, which was predicted to disappear from the Oosterschelde (Wolff & Sandee 1971).

The increased biodiversity caused by humans, could have large implications on the existing fauna. Arch-fronted swimming crab *Liocarcinus arcuatus* was recorded for the first time in the eastern part of the Oosterschelde in 1982 (Adema 1991a). During the period 1999-2001 it was the commonest swimming crab throughout the Oosterschelde. The success of *L. arcuatus* was probably related to its partly herbivorous feeding habit (Adema 1991a). Additionally, it was shown that *L. arcuatus* had less mobile chelipeds, which was reflected in a diet of sedentary prey without an exoskeleton, while the other swimming crabs were all pronounced carnivo-

rous species, which preyed primarily on mobile organisms with hard exoskeletons (Freire *et al.* 1996). Both macrophytes and macrobenthic prey were highly abundant in the Oosterschelde (van Berchum & Wattel 1997, Meire *et al.* 1991). Furtheron, *L. arcuatus* was the only crab species with a changed sex ratio from 1:1 to 3:1 females during the colder seasons, which could be advantageous for a rapid population growth.

More recently, Japanese brush crab *Hemigrapsus penicillatus*, a northeastern azian species is spreading quickly through Europe, and since 2000 it was recorded from the Oosterschelde and even from the Westerschelde (d'Udekem d'Acoz & Faasse 2002). In the Bay of Biscay *H. penicillatus* already became the commonest shore crab in many sheltered habitats, where it almost wiped out the entire population of *Carcinus maenas*.

During the 1970s starfish *Asterias rubens* was still recorded from the mouth of the Westerschelde (De Veen *et al.* 1979). It was shown that their ability to attach to the substrate decreased at salinities lower than 16 psu (Berger & Naumov 1996), but they are able to reproduce at salinities as low as 14 psu (Wolff 1968). The difference between both systems for *A. rubens* must be correlated with the discrepancy in food availability, namely the absence of its main prey blue mussel *Mytilus edulis* in the Westerschelde (in contrast to the Oosterschelde), which was attributed to the highly dynamic character of the Westerschelde estuary (Meire *et al.* 1991).

Also, hermit crab *Pagurus bernhardus* was uncommon in the Westerschelde and only recorded from the western part. The near absence could not be explained by a preference for higher salinities, nor by the high amounts of suspended matter (Wolff & Sandee 1971). Hermit crabs need gastropod shells for protection, large enough but not too heavy (Hazlett 1981). The different distribution of *P. bernhardus* in both systems might be correlated with the discrepancy in gastropod shell availability. Several gastropod species were highly abundant in the Oosterschelde (mainly *Littorina littorea*, *Nucella lapillus* and *Buccinum undatum*), but were not recorded from the Westerschelde (Meire *et al.* 1991, pers. observation).

5.4.3 Annual patterns in the macro-invertebrate composition

Both in the Oosterschelde and the Westerschelde, crabs and caridean prawns largely increased the species richness, although they were generally low in numbers of individuals. Shore crab *Carcinus maenas* and hermit crab *Pagurus bernhardus* were the more common species in the Oosterschelde. Also, in the Forth estuary (UK) *C. maenas* predominated the crab populations (Mathieson & Berry 1997). The success of *C. maenas* in the Oosterschelde is probably the result of a better survival of the larvae settling on complex substrate (Klein Breteler 1976). On the Swedish west coast the annual production of *C. maenas* was six times higher in areas with musselbeds, which proved that the abundance was highly dependent on the type of substratum (Pihl & Rosenberg 1982).

The caridean prawns *Palaemon serratus* and *Pandalus montagui* were relatively common throughout the Oosterschelde, although *P. serratus* is a typical southern species often found between macrophytes, while *P. montagui* is a typical northern species on loose sandy bottoms (d'Udekem d'Acoz 1999). *P. montagui* was the only prawn species next to *Palaemon longirostris*, caught in the western part of the Westerschelde. During the surveys of September and November 1988, it was noticed that respectively *P. montagui* and *Crangon allmanni* were 'common' between the bulk of *Crangon crangon* in the Oosterschelde, as well. It was quite remarkable that *Palaemon longirostris* was the second common species in the eastern part of the Westerschelde during 1999-2001. From hyperbenthic samples it was shown that at the end of the 1980s *P. longirostris* was not caught in the Westerschelde, while *Palaemonetes varians* was present at low numbers (Mees *et al.* 1995). At the end of the 1990s the inverse was seen, with several small juveniles of *P. longirostris* caught in summer and autumn with a hyperbenthic sledge (Chavatte 2001). In the lower part of the Schelde estuary *P. varians* was still the most abundant macrocrustacean species in 1995 (Maes *et al.* 1998a). In the Gironde estuary (France) juveniles and adults of *P. longirostris* mainly fed on mysid shrimps (Sorbe 1983), which are very abundant in the eastern part of the Westerschelde (Mees *et al.* 1993a). The presence of relatively high numbers of *P. longirostris* in the eastern part could point towards an improved habitat quality in the Westerschelde.

For the Thames estuary (UK), it was shown that several macro-crustacean species exhibited regular annual cycles in terms of density, correlated with seasonal changes in temperature or salinity (Attrill & Thomas 1996). For the Oosterschelde and the Westerschelde both multivariate analyses showed a clear seasonal pattern correlated with temperature and dissolved oxygen. Additionally, in the Westerschelde a spatial pattern was correlated with salinity and turbidity. However, Gibson *et al.* (1993) suggested that the annual cycles for several macro-crustacean species mainly resulted from recruitment and mortality, rather than from immigration and emigration in response to physical factors. The majority of estuarine opportunists drift as larvae from offshore waters into shallow coastal and estuarine nurseries (McLusky 1989, Little 2000). In a parallel study on the (mero)hyperbenthos, highest densities of zoeae and megalopae larvae of *Carcinus maenas*, *Liocarcinus holsatus*, *Pagurus bernhardus* and *Crangon crangon*

were recorded during spring in both the Oosterschelde and the Westerschelde, while the larval appearance of *Macropodia rostrata*, *Pisidia longicornis* and *Palaemon* species in the Oosterschelde was more or less confined to the summer period (Chavatte 2001). From the length-frequency distributions it was clear that most of the smallest juveniles of different crab, shrimp and echinoderm species were recorded during summer and spring. This resulted in peak densities of juveniles in summer for 13 and 5 species or in spring for 5 and 2 species in the Oosterschelde and Westerschelde, respectively.

In another study it was shown that higher densities of shore crab *Carcinus maenas* in the Westerschelde could be predicted by a combination of higher salinity, higher temperature and lower turbidity, while higher densities of brown shrimp *Crangon crangon* were predicted at moderate dissolved oxygen levels and only partly by higher temperatures (Chapter 6). Furtheron, these models fitted well the density patterns of both species in the Oosterschelde. In the latter system the regular annual cycle for *C. crangon*, with highest densities in summer, was masked by peak abundances of 18700 and 11800 ind/1000m² in winter 2000 at stations 33 and 35, respectively. In the other subareas and in 2001, the seasonal pattern was comparable with the Westerschelde. *C. maenas* immigrated as from spring throughout the whole Oosterschelde, where salinity was continuously higher than 30 psu. Although, lower densities were recorded during the colder seasons, and the low densities in the western and central part additionally correlated with the higher turbidity values in winter. The presence of berried females throughout the year (but mainly in spring), and of larvae both in spring and summer in the Oosterschelde (Chavatte 2001), was in agreement with the presence of different brood waves in the shallow coastal waters in Sweden (Pihl & Rosenberg 1982). In the Yealm estuary (UK) *C. maenas* individuals were spread throughout the estuary, except in summer when they were only found in the upstream part (McVean & Findlay 1979). In the Westerschelde an upstream migration was noted during summer, but for the other seasons the distribution of *C. maenas* was more or less confined to the western part, due to unfavourably low salinities in the eastern part.

Some of the macro-invertebrates only stayed for a short time in the estuarine areas. In the Oosterschelde 35% more species were recorded during the colder seasons, while the diversity in the Westerschelde increased with 30% during the warmer seasons. Seven out of nine caridean prawns did not occur in spring and summer in the Oosterschelde. The multivariate analyses showed a seasonal succession in the occurrence of different crab and shrimp species in the Westerschelde, and of most crabs and echinoderms in spring, caridean prawns in autumn-winter and cephalopods in summer in the Oosterschelde. For example, heart-urchin *Echinocardium cordatum* showed an average peak density in spring in the Oosterschelde, although this was only the case in 2000 (cf. the Canonical Correspondence Analysis). Possibly the spring peak of 2001 was missed due to the quarterly sampling scheme. In the Thames estuary (UK) flying crab *Liocarcinus holsatus* was only present in the summer samples (Attrill & Thomas 1996). Also, in the Westerschelde *L. holsatus* already disappeared after summer, while in the Oosterschelde it remained present at low densities till winter. This difference was correlated with the salinity pattern in both systems, where salinity was unfavourably low in autumn and winter in the Westerschelde. In an experiment it was shown that the sympatric swimming crabs *L. holsatus* and *L. depurator* showed endogenous circadian rhythms, with the first being more active during the day and the latter mainly active at night to minimize competitive interactions (Abello *et al.* 1991). This could also be the case in the Oosterschelde, although both species were rather spatially segregated. *L. holsatus* reached highest densities in the western part, while *L. depurator* was almost exclusively caught in the northern part. The latter species seemed to be more common offshore and only started to colonize the Oosterschelde since 1990 (Adema 1991a). Comparable with the Forth estuary (UK) (Mathieson & Berry 1997), males of *L. holsatus* outnumbered females by 2:1 both in the Oosterschelde and Westerschelde. For *L. depurator* modifications in the sex ratio from 1:1 could occur if many ovigerous females are present (Fernandez *et al.* 1991). This was not the case in the Oosterschelde, where the sex ratio stayed around 1:1during all seasons, even in spring when most berried females were caught.

5.4.4 Interannual versus longterm patterns

Comparable with the end of the 1980s, high densities of brown shrimp *Crangon crangon* and starfish *Asterias rubens* were caught in the Oosterschelde during the period 1999-2001, while *C. crangon* predominated in the Westerschelde. Also, in other coastal systems the catches of invertebrates were dominated by these species (*e.g* Rogers 1994). However, the brittlestar *Ophiura ophiura* (and *Ophiura albida*) outnumbered all other species in the Oosterschelde. The success of the ophiuroids can be attributed to their motility, small size and ability to utilize the protective cover of natural retreats (Barnes 1987). *O. ophiura* and *Ophiothrix fragilis* were found to be the commonest brittlestars in coastal areas of the North Sea during the 1960s, with *O. ophiura* preferably found on soft sediments (Wolff 1968). Around the British Isles (UK) 2 ophiuroid species covered the substratum at densities up to thousands per m² at the end of the 1980s (Aronson 1989). Still, brittlestars are known to show a high interannual vari-

ability (Wolff 1968). A huge increase in densities of *O. fragilis* on hard substrata (layers up to 5 cm) in 1988-89 was attributed to the succession of several mild winters, while after even a short but cold winter (*e.g* 1990) the population of brittlestars was strongly reduced (Leewis *et al.* 1994). During the study period 1999-2001 the temperature never dropped below zero, which could explain the huge densities of *O. ophiura* recorded in the western part of the Oosterschelde during the 3 successive years. Though, for the second half of 2001 densities were much lower than in 1999 and 2000.

Still, longterm distribution patterns were apparent but quite different in both ecosystems. The average density and biomass of the 4 macro-invertebrate species that could be compared between 1988-89 and 1999-2001 largely increased in the Oosterschelde, while in the Westerschelde the average density largely decreased for *Crangon crangon* and *Liocarcinus holsatus* and more or less stayed the same for *Carcinus maenas*. In the Forth estuary (UK) all crab species increased between 1985 and 1995, due to changed industrial practices since the early 1980s (Mathieson & Berry 1997). *L. holsatus* is rather uncommon in real estuaries with fluctuating salinities. It remains unclear why De Veen *et al.* (1979) reported relatively high densities in the western part of the Westerschelde during the 1970s, in contrast to the present and previous studies (*e.g* Wolff & Sandee 1971).

In a parallel study it was shown that in the eastern part of the Oosterschelde the average densities for at least 16 fish species (a.o. the gadoid and flatfish species) drastically declined in 1999-2001 compared to 1987-89, which was attributed to the increased presence of allochtonous drifting macrophytes (several species) and japanese oysters *Crassostrea gigas* (Chapter 4). A reduced habitat quality caused by these factors, could partly explain the low densities of flying crab *Liocarcinus holsatus* and starfish *Asterias rubens* in the eastern part. A reduced habitat quality was probably also the cause of the low average densities of both species in 1988-89 (except in summer for *A. rubens*) in this part of the Oosterschelde. On the other hand, the eastern part carried high average densities of *Carcinus maenas* and *Crangon crangon*. For the other species no indication of a deterioration or improvement could be given, but the caridean prawns *Palaemon adspersus* and *Palaemon elegans* were almost exclusively found in the eastern part during 1999-2001.

Furtheron, 11 macro-invertebrate species reached higher average densities in either or both the western and northern part of the Oosterschelde. For a number of species this was indirectly related with the muddy bottom in the northern part and at station 10 in the western part. Freire *et al.* (1990) showed that the sediment structure could be transformed by mussel detritus. Due to a changed cultivation regime, the sublittoral area (especially in the western part) became very important growing areas for blue mussel *Mytilus edulis* (Smaal & Lucas 2000). The increase of starfish *Asterias rubens, Carcinus maenas* and *Liocarcinus holsatus* in the Oosterschelde compared to 1988-89, was mainly attributed to this increased food resource. A massive outbreak and subsequent decline of *A. rubens* in the Bay Douarnenez (France) was related to food availability (bivalves), predation (other starfish) and changing temperatures (Guillou 1996). In the ebb-tidal delta of the Grevelingen (Netherlands) the starfish population drastically declined from 1989 to 1993, possibly related to a decreased prey density (Hostens, unpubl. data). Additionally, the large intertidal flats with high biomasses of macrobenthic molluscs, annelids and crustaceans (Coosen *et al.* 1994, Ysebaert *et al.* 1993) could be seen as important food resources, and surely contribute to the high densities of several mobile macro-invertebrate species throughout the Oosterschelde and the Westerschelde. Also, the destruction by and discards from the extensive shellfisheries on mussels, cockles and oysters throughout the Oosterschelde, possibly attracted scavenging species. In Red Warf Bay (UK) predators like *Pagurus bernhardus*, *Asterias rubens* and *Ophiura ophiura* responded to the trawling activities by feeding on damaged bivalves, echinoderms, crustaceans and polychaetes (Ramsay *et al.* 1998).

The discrepancies for *C. crangon* between the Oosterschelde and the Westerschelde could be explained in several ways. In a previous study it was shown that the average biomass showed a fourfold decrease from 1984-85 to 1988-89 in the Oosterschelde, attributed to a decreased nutrient input and an increased gadoid population (Chapter 3). Similar to the present study, the Demersal Young Fish Surveys (RIVO, NL) found much lower shrimp densities in the Oosterschelde compared to the Westerschelde in 1988 and 1989, while in both systems the autumn densities were low in 1990 and conversely high in 1992 (Daan 1995). Together with the results of van Beek & Boddeke (1990) it could be concluded that the strong yearly fluctuations during the 1970s and 1990s were comparable between both systems, while the construction of the storm-surge barrier led to a disturbed distribution during the 1980s in the Oosterschelde. Furtheron, shrimp densities in the Oosterschelde always have been lower compared to the Westerschelde (Daan 1995). This was also the case in 1999-2001, despite the threefold increase in the first system and the decline in the latter compared to the period 1988-89. Intertidal habitats are important nurseries for the pre-recruits of *C. crangon* (and possibly other macro-invertebrates). Therefore, a relation with the smaller area of essential intertidal habitat in the Oosterschelde compared to the Westerschelde, is suggested. Additionally, the shortterm interannual variability largely masks the - probably underesti-

mated - longterm negative impact of an irreversible and ongoing reduction of intertidal habitat, due to the construction of the storm-surge barrier in the Oosterschelde (ten Brinke *et al.* 1994, van Berchum & Wattel 1997) and the dredging and dumping activities in the Westerschelde (Vroon *et al.* 1997, Anonymous 1998).

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CHAPTER 6 FISH AND MACRO-CRUSTACEAN RESPONSE SURFACES TO ENVIRONMENTAL GRADIENTS IN THE WESTERSCHELDE ESTUARY

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Abstract. *Juvenile fish and macro-crustaceans of the Westerschelde were intensively sampled with a 3-metre beam trawl in the periods 1988-91 and 1999-2001. Models were developed to predict the occurrence and density of the 15 commonest species in response to a limited set of environmental variables. Single logistic regressions yielded good descriptions of the occurrence of any one species along one environmental gradient. This was related to the maximum likelihood of presence in the field, although several species showed a broad tolerance towards one or more of the 4 environmental variables used. The response curves should only be interpreted as actual distribution patterns of juvenile fish and macro-crustaceans as a function of the four environmental variables. Multiple logistic regressions and normal regressions gave insight into the relative importance of each environmental variable for every single species. All response surfaces, either based on presence/absence or on density data, were highly significant when combining data on temperature, salinity, turbidity, dissolved oxygen concentration and/or their quadratic effects. The addition of other, extrapolated variables (current velocity, mysid prey density, chlorophyll a or suspended particulate matter) did not improve the predictions. For most species the prediction of presence/absence was relatively successful (60-90 % correctly predicted). Sensitivity (% present predicted as present) and specificity (% absent predicted as absent) were equally high in most models, and validation proved the models to be accurate and robust. The models that predicted density patterns could only explain between 20-55 % of the variance. Best 'density' models were built for those species that were present in the estuary during a longer period with only one clear density peak, i.e. Limanda limanda, Pomatoschistus microps, Carcinus maenas, Liocarcinus holsatus, Platichthys flesus, Sprattus sprattus and Pomatoschistus minutus. The least models concerned species belonging to the ecological guild of 'marine juveniles' (e.g. Trisopterus luscus, Merlangius merlangus, Clupea harengus, Solea solea and Pleuronectes platessa). Also, the 'density' models for Crangon crangon, Syngnathus rostellatus and Pomatoschistus lozanoi were less successful. Temperature (and dissolved oxygen concentration) mainly reflected seasonal effects, while salinity and turbidity reflected spatial effects. Still, it is argued that the interaction between several environmental variables (e.g. temperature and salinity) was even more important in predicting species occurrence and density.*

6.1 Introduction

The ecology of estuarine fish and macro-crustaceans has been thoroughly studied. Several studies have shown the importance of estuaries as nursery and wintering sites, migration routes, and areas which naturally support high densities of fish and macro-crustaceans (overview in Elliott & Hemingway 2002). Strong environmental gradients prevent most animals from the adjacent sea or rivers to enter the estuarine ecosystems (McLusky 1989). Following the concept of ecological guilds (Elliott & Dewailly 1995), 24 fish species in the Westerschelde were

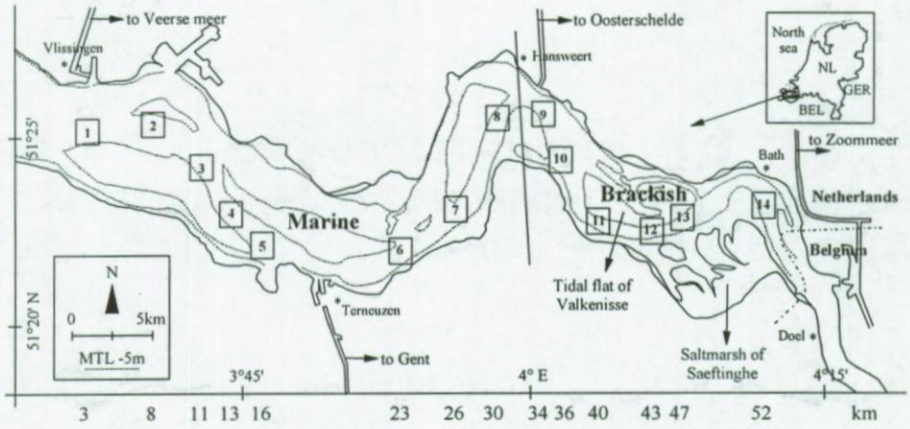

Fig. 6.1 Map of the Westerschelde estuary with 14 sampling locations in the subtidal channel

classified as marine species, 8 as estuarine resident and 5 as diadromous species (Chapter 2).

During the past decades, both seasonal and spatial patterns in fish and macro-crustacean assemblages have been uncovered in different holarctic estuaries, by means of multi-species analyses (*e.g* Elliott & Dewailly 1995, Blaber 1997, Potter *et al.* 1997). Several studies showed that a number of species was present during only a short period, with a clear cyclical succession in time, related to seasonal changes in the environment and to intra-annual and seasonal changes in appearance of several species (Thiel & Potter 2001, Chapter 2). Spatial differences in the distribution pattern of the fish and macro-crustacean assemblages within estuaries, were mainly related to salinity, the degree of exposure and the type of substratum (Henderson 1989, Chapter 2-Add.2).

For management purposes it is necessary to be able to predict the occurrence and distribution of both commercial and non-commercial fish and macro-crustacean species in the estuary. Single-species models can extend the knowledge of the species-environment relationships (Attrill *et al.* 1999). Most probably, single fish and macro-crustacean species within the ecological guilds will respond differently to changes in the surrounding environment. These so-called response curves (to changes in one variable) and surfaces (to combined changes in several variables) can be fitted through mathematical relations (Austin 1987), but the models should be simple to be useful (Bourget *et al.* in press). Logistic regression has been applied in the field of estuarine animal ecology since the mid 1990s (Ysebaert *et al.* 2002).

Several experimental studies generated species tolerance levels to physical factors (overview in Elliott & Hemingway 2002), but few attempts have been made to statistically model trends in abundance for individual crustacean and fish species in the field (Attrill *et al.* 1999, Power *et al.* 2000b). Most biological data sets lack corresponding environmental data, which are necessary to establish conclusions on possible controlling factors. During a period of 4 years and a period of 3 years two 'complete' data sets (with both species and environmental data) have been collected from the Westerschelde (Hostens *et al.* 1996, Hostens unpubl. data).

In this paper, the hypothesis is tested whether a limited set of environmental variables can be used to predict presence/absence and density patterns of the commonest fish and macrocrustacean species in the Westerschelde. It is argued that the used environmental variables adequately represent the seasonal and spatial variation in the estuary and are sufficient to build significant models.

6.2 Material and methods

6.2.1 Sampling methodology

The Westerschelde (55 km, 310 km²) consists of the lower and middle reaches of the Schelde estuary, situated in the southwest part of the Netherlands (Fig. 6.1). It is a well mixed, multiple channel system (average depth between 15 and 20 metres below Mean Tidal Level (MTL)), with large intertidal areas (35% of the area) and subject to large tidal fluctuations (up to 5 metres). Maximum ebb and flood current velocities vary between 2 and 3 knots at average neap and spring tide respectively (recalculated from Anonymous 1992). It is a turbid nutrient-rich and polluted area, under high pressure from dredging activities for shipping purposes. The ecological and environmental properties of the Westerschelde estuary are explained in detail in Meire & Vincx (1993) and Heip & Herman (1995).

Fish and macro-crustaceans were sampled at 14 locations in the main subtidal channel of the Westerschelde estuary (Fig. 6.1). Surveys were repeated monthly between January 1988 and December 1991 and continued on a quarterly basis between

September 1999 and May 2001. August 1988 was sampled twice; May and September 1991 were not sampled. This resulted in 55 surveys and 734 sampling points. A 3-m beam trawl (5x5 millimetres mesh-size in the cod end) was towed over a distance of 1000 m with the R.V. Luctor (34 m, 500 Hp). Sample methodology was fully described in Chapter 2. In summary, fish species were counted and measured, while crustaceans were counted and/or weighed in bulk. Densities were expressed as numbers per 1000 m^2, assuming a 20 % net-efficiency (see Chapter 3). For the present study, the data of the commonest species, 12 fish and 3 macro-crustacean species, were used (Chapter 2), belonging to the clupeoids (herring *Clupea harengus* and sprat *Sprattus sprattus*), the gadoids (whiting *Merlangius merlangus* and bib *Trisopterus luscus*), Nilsson's pipefish (*Syngnathus rostellatus*), gobiids (common goby *Pomatoschistus microps*, sandgoby *P. minutus* and Lozano's goby *P. lozanoi*), flatfish (plaice *Pleuronectes platessa*, dab *Limanda limanda*, flounder *Platichthys flesus* and sole *Solea solea*), crabs (flying crab *Liocarcinus holsatus* and shore crab *Carcinus maenas*) and brown shrimp (*Crangon crangon*).

Four environmental variables were measured at each sampling point: temperature (°C), dissolved oxygen content ($mg.l^{-1}$), salinity (psu) and turbidity (m^{-1}). The first three were measured near the bottom, whereas turbidity was calculated as the reciprocal of Secchi-depth. Data on other possible determinants were not available, were not measured near the bottom or overlapped only partly with the biotic sampling data. Most samples were taken around spring tide or at an average tidal level. Current velocity was estimated as the average tidal current in the upper water layer in the vicinity of every sampling point, given in hourly intervals in reference to high water near Vlissingen at spring and neap tide in the current atlas (Anonymous 1992), and from the difference between time of sampling and time of high water near Vlissingen. Sampling was only possible below 3 Beaufort, thus the influence of changing weather conditions on the current velocity was considered to be minimal at the moment of sampling. Also, some biological variables were included. For 110 corresponding sampling points, densities of a major prey group, namely the Mysidacea were taken from Mees (1994) and Chavatte (2001). Monthly data on Chlorophyll *a* and suspended particulate matter in the water column near the sampling points were made available through the Centre for Estuarine and Marine Ecology (Yerseke, The Netherlands).

6.2.2 Modelling details

The Generalized Linear Model concept has the advantage that the distribution of the dependent variable does not have to be continuous and the effect of the predictors on the dependent variable can be made linear through link functions (McCullagh & Nelder 1989). All regression equations were established with the statistical package Statistica, which gives an exhaustive explanation of the used techniques (StatSoft 1995).

Second-order polynomials (or quadratic effects) were included in the regressions to achieve gaussian probability functions as response curves and surfaces, which are ecologically more relevant in most cases (Ter Braak & Looman 1986). In the generalized model the response variable Y is linearly associated with values on the X environmental variables by:

$$Y = g\,(b_0 + b_1X_1 + b_2X_1^2 + b_3X_2 + b_4X_2^2 + \ldots + b_{k-1}X_k + b_kX_k^2) + e \quad (1)$$

where e stands for the error variability not accounted for by the predictors (expected to be 0), b_0 is the regression coefficient for the intercept and the b_i values are the regression coefficients (for variables 1 through k) computed from the data. The inverse function of $g(...)$ is called the link function; so that:

$$f(z_y) = b_0 + b_1X_1 + b_2X_1^2 + b_3X_2 + b_4X_2^2 + \ldots + b_{k-1}X_k + b_kX_k^2 \quad (2)$$

where z_y stands for the expected value or the probability of y, which is bound between 0 and 1.

6.2.3 Presence/Absence models

In a first series of models the density values were reduced to binary data to predict the probability of occurrence of the 15 species as a function of the *a priori* selected environmental variables. Presence/absence data show less variation and are easier to predict than real numbers. For these models the logit link function is used, where $f(z_y) = \log(z_y/(1-z_y))$.

So, equation (2) can be rewritten as:

$$z_y = e^{(b0 + b1X1 + b2X1^2 + b3X2 + b4X2^2 + \ldots + bk\text{-}1Xk + bkXk^2)} / \{1 + e^{(b0 + b1X1 + b2X1^2 + b3X2 + b4X2^2 + \ldots + bk\text{-}1Xk + bkXk^2)}\} \quad (3)$$

The values of the parameters (b_0 through b_k and the scale parameter) in the generalized linear model were obtained by maximum likelihood estimation. The significance of the models was tested with the –2logL statistic, where the maximized likelihood L approximates a *Chi-square* distribution. The Wald statistic (*Chi-square*, $p<0.05$) was used to test the significance of the regression coefficients.

Single logistic regressions showed the probability of occurrence of the 15 species as a response to each of the 4 environmental variables separately. Linear models were presented when the quadratic effects did not have significant explanatory power.

Next, the presence/absence of the fish and macro-crustacean species was predicted by multiple logistic regressions, where all variables (and their quadratic effects) were entered (or rejected) in the models by means of forward stepwise selection. The resulting presence/absence models (or response surfaces) were validated in several ways. Therefore, the estimated probabilities (on a continuous scale between 0 and 1) were back-transformed to binary data. A threshold p-value was determined for every model as the ranked probability value that corresponded with the observed ratio between presences and absences. Probabilities higher than that p-value were considered to predict presence, while lower values predicted a species to be absent. In this way, the predictive success (percentage correctly predicted), specificity (percentage absent predicted as absent) and sensitivity (percentage present predicted as present) could be calculated.

These diagnostics were calculated for the final models and for five model runs per species with a random selection of 50 % of the data, to evaluate the robustness and classification accuracy of the final models. The 50 % model equations were used in cross-validations with the other half of the respective data sets and with a randomly generated set of 1000 values per environmental variable (within the observed limits of these predictors). For the random environmental sets, linear correlation coefficients between five model runs were calculated.

6.2.4 Density models

In a second approach single-species regression models were based on log-transformed data (calculated as the natural logarithm of density +1 per 1000 m²), to approximate normal distributions. Therefore, an identity link function could be used, where $f(z_y) = z_y$, and equation (2) is appropriate to predict the response surfaces of species abundance by a linear combination of the environmental data. The shape of the response curves (and surfaces) is dependent on the sign of the actual regression coefficients (b) and the ratio between the absolute beta-values of the linear and quadratic effects (i.e. the relative magnitude of both effects) (Fig. 6.2).

The model equations were built with the General Stepwise Regression module in Statistica (StatSoft 1995). From an explorative analysis with all environmental variables, the sample points for every single species for which the predicted values deviated more than 60% from the observed values, were considered to be outliers and were eliminated from further analyses. For the final 'density' models, quadratic regression designs and forward stepwise selection of the environmental variables were used. Assumptions on normality and homogeneity of the residuals were graphically inspected. Standardized regression coefficients (ß) indicate the magnitude of

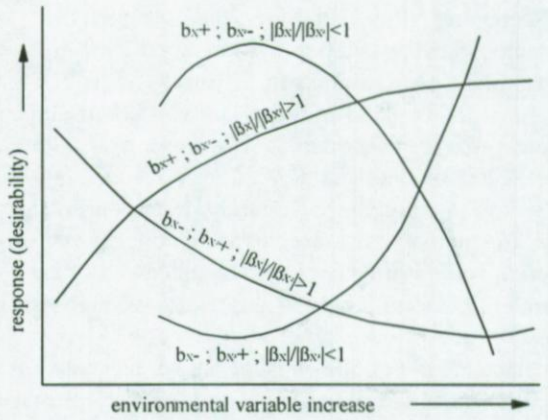

Fig. 6.2 Simplified response curves of a dependent variable, dependent on the signs of the actual regression coefficients (b) and the ratio between the standardized regression coefficients (ß) for the linear and quadratic effects of any independent variable

the contribution of each withdrawn effect ($p < 0.05$) to the final models. The fit of the regression surface as defined by the predicted values and the estimation of the effects included in the final models were based on the least squares method. Type VI (effective hypothesis) sums of squares can deal with missing cells and provide an unambiguous estimate of the variability of the predicted values attributed to each effect (Hocking 1996).

6.3 Results

6.3.1 Environmental gradients

Both spatial and temporal patterns in the environmental variables are given in Fig. 6.3. Temperature mainly showed a seasonal trend, with summer peaks (averaged 19 °C) and winter troughs (averaged 6 °C), and a cold February 1991 (<1 °C). The upstream part of the Westerschelde was on average 1 degree warmer than the most marine sampling location in a more or less linear trend. An important spatial pattern in the Westerschelde was shown by the linear salinity gradient (averaging between 28 and 13 psu, with minimum and maximum values of 4 and 32 respectively). River runoff clearly showed downstream freshwater intrusions during the winter periods, with low values in 1988. The Westerschelde was well saturated with oxygen (on average between 7 and 11 $mg.l^{-1}$), but oxygen levels linearly dropped with on average 3 units from the marine to the brackish stations with minima between 3 and 5 $mg.l^{-1}$ in the most upstream station 14 (near the Dutch-Belgian border). The seasonal pattern showed high oxygen concentrations during the winter period, with extreme values (maximum 14 $mg.l^{-1}$) in 1991. The seasonal pattern in turbidity resembled the oxygen pattern (averaging between 0.8 and 2.2 m^{-1}), while the spatial pattern showed an opposite gradient with higher values in

the upstream part (up to 5 m^{-1}). Both ebb and flood current velocities at the moment of sampling varied between 0 and 3 knots (= 1.5 $m.s^{-1}$), without a clear seasonal pattern. In most cases the current velocity was higher in the middle reaches of the Westerschelde between stations 9 and 12.

Mysid prey densities were on average 2 m^{-2}, exponentially increasing towards the brackish reaches, with a maximum up to 160 m^{-2} during summer (Mees 1994, Hostens unpubl. data). Chlorophyll *a* concentrations varied between 0.3 and 45 $\mu g.l^{-1}$ with a clear seasonal peak during spring. SPM values ranged between 4 and 440 $mg.l^{-1}$ (on average 50 $mg.l^{-1}$), without a clear seasonal or spatial trend. (Chl*a* and SPM data from CEME, the Netherlands).

6.3.2 Single-species response curves

In total, 49 of the 60 single logistic regressions were highly significant. No significant relations were found for brown shrimp *Crangon crangon.*

Five species had a higher probability of occurrence at low temperatures (Fig. 6.4). For *Clupea harengus, Pleuronectes platessa* and *Platichthys flesus* the difference was rather small, but the response curves for *Pomatoschistus microps* and *Limanda limanda* showed a steep decline at temperatures above 12 °C. Four species were predicted to occur at higher temperatures (*Trisopterus luscus, Solea solea, Carcinus maenas* and *Liocarcinus holsatus*. Three species (*Merlangius merlangus, Syngnathus rostellatus* and *Pomatoschistus lozanoi*) showed a bell-shaped curve with an optimum at intermediate temperatures. The opposite holds for *Sprattus sprattus* and *Pomatoschistus minutus*, with increasing probabilities towards the lower and upper end of the temperature range.

Most species showed a linear response and a broad tolerance in relation to salinity. Nine species likely occurred at higher salinities, but only the 2 crab species were clearly limited with a probability of occurrence of more than 50 % at salinities above 15 psu for *C. maenas* and above 27 psu for *L. holsatus*. Four species (*C. harengus, P. microps, P. flesus* and *S. solea)* were predicted to occur at lower

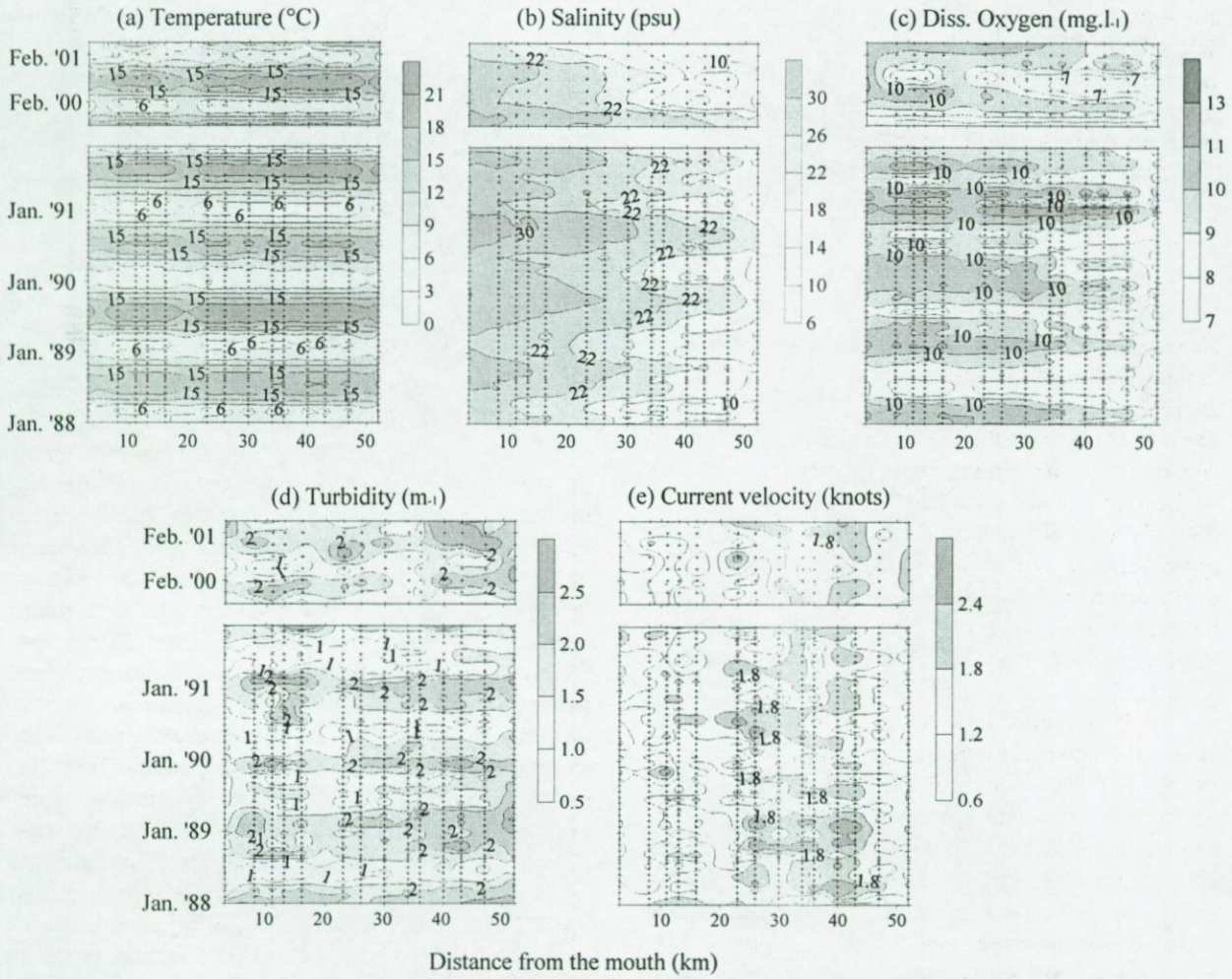

Fig. 6.3 Spatio-temporal contour plots for 5 environmental variables. The abscis represents the spatial variation based on the 14 sampling points; the temporal axis shows 48 monthly surveys between January 1988 and December 1991, and 8 quarterly surveys between September 1999 and May 2001

salinities.

Five response curves to dissolved oxygen concentrations were insignificant. Three species (*S. sprattus*, *P. microps* and *P. platessa*) had a higher probability to be found at higher oxygen levels. For *T. Luscus*, *P. minutus* and *S. solea* the opposite was predicted. Four species differed in their tolerance and in the position of their optimum towards the upper (*L. limanda*), the middle (*M. merlangus*), the lower (*S. rostellatus*) or both (*P. flesus*) ends of the oxygen range.

Four response curves showed a higher probability to occur at higher turbidities for four species (*C. harengus*, *S. sprattus*, *P.* platessa and *P. flesus*). Five species were predicted to have a low tolerance towards turbidity, with probabilities of more than 50% at turbidity values <1 m^{-1} for *M. merlangus*, *T. luscus*, *S. rostellatus* and *L. holsatus,* and <2.5 m^{-1} for *C. maenas*. Four other species showed gaussian logit response curves with an optimum towards lower turbidities (*P. minutus* and *P. lozanoi*) or towards higher turbidities (*P. microps* and *L. limanda*).

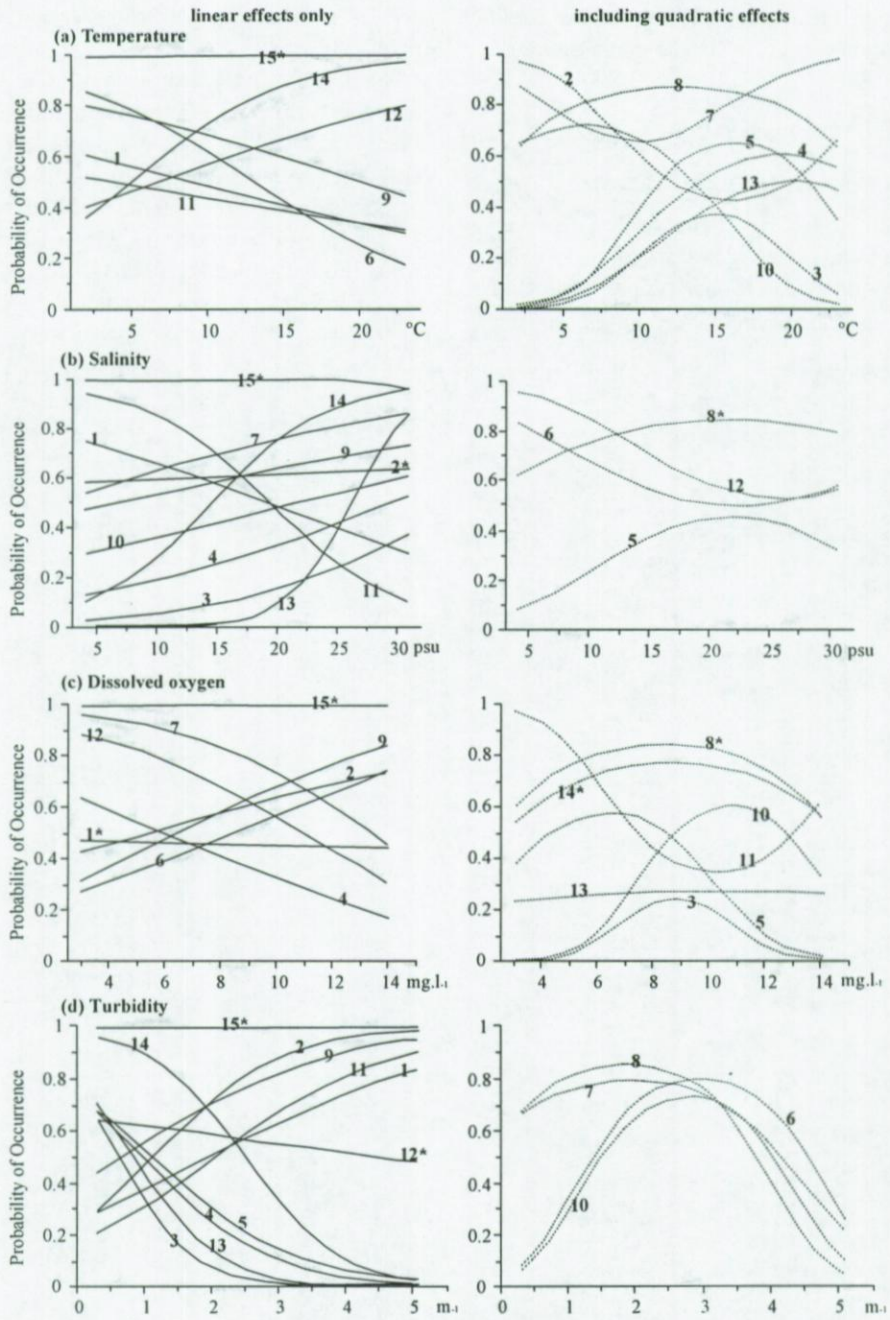

Fig. 6.4 Probability of occurrence fitted with logistic regressions in relation to each of the 4 environmental variables. Linear response curves are given, if the quadratic effects were insignificant. Line numbers correspond with: (1) *C. harengus*, (2) *S. sprattus*, (3) *M. merlangus*, (4) *T. luscus*, (5) *S. rostellatus*, (6) *P. microps*, (7) *P. minutus*, (8) *P. lozanoi*, (9) *P. platessa*, (10) *L. limanda*, (11) *P. flesus*, (12) *S. solea*, (13) *L. holsatus*, (14) *C. maenas*, (15) *C. crangon*. Insignificant regressions were indicated with an asterisk*

Table 6.1 Ecological guild and some diagnostics for the final Presence/Absence models: actual numbers absent and present, -2logL statistic for 'the intercept only' (I) and for 'the intercept with covariates' (I+C), *chi-square*, percentage explained variance, and different environmental variables successively retained in each model

Species	Guild [1]	# Absent	# Present	-2logL		Chi²	%Var	Selected variables [2]
				I	I+C			
Clupea harengus	MJ	397	334	1008	957	51	5	S T T²
Sprattus sprattus	MS	281	450	974	823	151	16	T T² S Tu O² O
Merlangius merlangus	MJ	589	142	720	598	122	17	Tu Tu² S
Trisopterus luscus	MJ	469	262	954	775	179	19	T S T²
Syngnathus rostellatus	ER	441	290	982	791	191	19	T T²
Pomatoschistus microps	ER	336	395	1009	854	155	15	T Tu Tu² S²
Pomatoschistus minutus	ER	171	560	795	656	139	18	S T² T O² Tu O Tu²
Pomatoschistus lozanoi	MS	133	598	693	669	25	4	Tu Tu² T T²
Pleuronectes platessa	MJ	259	472	950	886	65	7	S Tu T
Limanda limanda	MJ	370	361	1013	736	278	27	S² Tu T² Tu² T
Platichthys flesus	ER	425	306	994	820	174	17	S Tu²
Solea solea	MJ	291	440	983	893	90	9	T S T² S²
Liocarcinus holsatus	MJ	532	199	856	414	442	52	S T O²
Carcinus maenas	ER	184	547	825	569	256	31	S T
Crangon crangon	ER	3	728	39	32	7	18	S²

Note: [1] MJ (marine juveniles), MS (marine seasonal/adventitious), ER (estuarine resident) species
[2] T (temperature), S (salinity), O (oxygen), Tu (turbidity) and their corresponding quadratic effects

6.3.3 Presence/Absence modelling diagnostics

As none of the other (extrapolated) environmental variables were withdrawn in the stepwise procedure, the final multiple regressions for the 12 fish and 3 crustacean species were limited to the four main environmental variables (temperature, salinity, oxygen, turbidity, and their quadratic derivations). According to the Wald statistic, temperature and salinity appeared as important variables to predict species occurrences in almost all models, followed by turbidity for 8 models and oxygen for 3 models (Table 6.3). All final logistic models were highly significant ($p << 0.001$) based on the *chi-square* test. The explained variance can be calculated as 1 minus the ratio of the –2logL statistics for the intercept with covariates and the intercept-only model (Table 6.1). Around 50 % of the variance could be explained for *L. holsatus*, around 30 % for *L. limanda* and *C. maenas*, and around 20 % in 8 other models.

Threshold-P values (above which calculated probabilities were converted to presences) were around 0.5 and higher (Table 6.2), which corresponded with the actual ratio of absence and presence

Table 6.2 Threshold-p values, predictive success (% correct), specificity (% absent predicted as absent) and sensitivity (% present predicted as present) for the 15 final presence/absence models. The same diagnostics are given as averages (± std) for each time five fitted models with 50% of the data and five cross-validations of these 50% models with the rest of the data. The last column shows the range of linear correlation coefficients between five fitted models, based on the equations from the 50% models and 1000 random values for each environmental variable

Species	Final P/A model				50% data fitting			50% cross-validation			Correlation
	ThresP	%corr	%AasA	%PasP	%corr	%AasA	%PasP	%corr	%AasA	%PasP	
Clupea harengus	0.46	62	64	59	62 (1.9)	65 (2.0)	59 (3.3)	60 (2.3)	62 (3.3)	58 (2.9)	0.96-0.99
Sprattus sprattus	0.52	70	60	77	70 (1.5)	60 (9.6)	76 (8.1)	70 (1.5)	60 (1.6)	76 (1.6)	0.83-0.95
Merlangius merlangus	0.33	81	88	52	83 (1.1)	89 (1.1)	54 (1.0)	78 (1.2)	86 (1.1)	50 (2.1)	0.89-0.95
Trisopterus luscus	0.52	73	79	62	73 (2.5)	79 (2.1)	62 (3.4)	72 (2.7)	77 (2.0)	62 (4.2)	0.90-0.96
Syngnathus rostellatus	0.58	69	73	62	69 (1.2)	73 (1.8)	62 (5.2)	69 (0.7)	74 (0.8)	62 (1.5)	0.92-0.99
Pomatoschistus microps	0.53	71	69	73	72 (1.9)	70 (2.3)	74 (2.5)	70 (1.6)	66 (2.2)	73 (2.0)	0.84-0.99
Pomatoschistus minutus	0.65	80	53	88	81 (2.7)	57 (5.8)	88 (1.7)	77 (0.7)	51 (3.7)	85 (0.4)	0.84-0.98
Pomatoschistus lozanoi	0.77	74	29	84	75 (1.1)	29 (5.0)	86 (1.4)	74 (0.7)	27 (5.1)	85 (1.0)	0.97-0.99
Pleuronectes platessa	0.58	66	51	73	67 (1.7)	53 (3.6)	75 (1.3)	65 (1.8)	49 (4.2)	74 (1.3)	0.96-0.99
Limanda limanda	0.55	77	78	77	78 (0.9)	78 (1.2)	77 (0.7)	77 (1.3)	77 (1.3)	78 (1.6)	0.84-0.99
Platichthys flesus	0.43	72	76	67	70 (1.7)	74 (1.9)	64 (2.7)	74 (1.9)	77 (1.8)	69 (2.7)	0.93-0.99
Solea solea	0.62	65	56	71	62 (1.3)	52 (3.8)	69 (1.0)	66 (1.7)	55 (1.9)	73 (1.5)	0.92-0.99
Liocarcinus holsatus	0.46	87	91	76	88 (0.8)	92 (0.5)	78 (2.8)	86 (0.5)	90 (0.5)	75 (1.4)	0.85-0.92
Carcinus maenas	0.61	80	60	87	80 (2.2)	60 (2.6)	86 (1.7)	81 (2.1)	60 (2.9)	88 (1.7)	0.98-0.99
Crangon crangon	0.94	99	0	100	99 (0.9)	-	99 (0.6)	92 (11.4)	-	93 (11.7)	0.92-0.95

Table 6.3 Regression coefficients and the Wald statistic between brackets ($p < 0.05$ if Wald >5) for the intercept and the withdrawn environmental variables (including the quadratic effects) for 15 'presence/absence' models (from which the probability of occurrence can be calculated as in formula 3, see text)

Species	Intercept	Temperature	Salinity	Oxygen	Turbidity	Temperature²	Salinity²	Oxygen²	Turbidity²
Clupea harengus	2.9 (28.7)	-0.26 (8.7)	-0.07 (25.4)	-	-	0.01 (5.7)	-	-	-
Sprattus sprattus	-1.66 (0.6)	-0.75 (33.8)	0.08 (19)	1.26 (8.7)	0.7 (15.1)	0.02 (25.2)	-	-0.08 (12.6)	-
Merlangius merlangus	0.98 (1.8)	-	0.05 (6)	-	-3.6 (47)	-	-	-	0.64 (21.7)
Trisopterus luscus	-6.42 (61.9)	0.56 (20.3)	0.06 (15.5)	-	-	-0.01 (9.3)	-	-	-
Syngnathus rostellatus	-6.77 (74.4)	0.91 (48.3)	-	-	-	-0.03 (31.9)	-	-	-
Pomatoschistus microps	-1.73 (6.9)	-0.1 (30.9)	-	-	2.55 (25.7)	-	0 (3.9)	-	-0.45 (13.2)
Pomatoschistus minutus	-6.15 (5)	-0.74 (28)	0.13 (39.7)	1.77 (10.6)	2.41 (15)	0.03 (34.7)	-	-0.12 (17.7)	-0.46 (9.7)
Pomatoschistus lozanoi	-2.25 (6.5)	0.36 (12.4)	-	-	2.08 (13.7)	-0.01 (11)	-	-	-0.51 (13.3)
Pleuronectes platessa	-1.81 (9.1)	-0.04 (5.8)	0.08 (28.2)	-	0.77 (20.7)	-	-	-	-
Limanda limanda	-7.03 (47.8)	0.46 (19.3)	-	-	3.74 (37.3)	-0.03 (34)	0 (63.9)	-	-0.68 (20.4)
Platichthys flesus	3.16 (59.3)	-	-0.18 (107.4)	-	-	-	-	-	0.1 (7.3)
Solea solea	2.43 (4.5)	0.37 (15.5)	-0.37 (13.1)	-	-	-0.01 (8.5)	0.01 (8.2)	-	-
Liocarcinus holsatus	-19.72 (130)	0.37 (87.9)	0.51 (125.4)	-	-	-	-	0.02 (8.2)	-
Carcinus maenas	-5.16 (109.2)	0.2 (75.5)	0.21 (104.3)	-	-	-	-	-	-
Crangon crangon	11.34 (10.8)	-	-	-	-	-	-0.01 (4.2)	-	-

(Table 6.1). For five species >80 % and for seven other species >70 % of the occurrences could be correctly predicted with the final models. Sensitivity fluctuated around 70 % and specificity was moderate to high, except for *P. lozanoi* and *C. crangon* where <40 % of the absences were predicted to be absent. Model fitting with only 50 % of the data proved to be consistent with the final models. Cross-validation of these 50%-models with the corresponding rest of the respective data achieved similar results. Model testing with random values for the environmental variables showed high correlation coefficients in a pairwise comparison between the five models for every species, ranging between 0.83 and 0.99 (Table 6.2).

6.3.4 Density modelling diagnostics

All 15 multiple stepwise regressions were highly significant ($p < 0.0001$), and seven models could explain between 58 and 45 % of the variance, i.e. for *L. limanda, P. microps, C. maenas, L. holsatus, P. flesus, S. sprattus* and *P. minutus* (Table 6.4). The other models explained between 22 and 37 % of the variance. All included regression coefficients were highly significant, except for the intercept in the models for *S. sprattus, C. maenas* and *C. crangon.* Temperature and salinity (and/or their quadratic effects) were selected in most models, while oxygen

Table 6.4 Actual (b) and standardized (ß) regression coefficients and t-values ($p < 0.05$ if $t > 2$), for the intercept and the withdrawn environmental variables (including the quadratic effects), next to the F and R^2 statistics for the 15 'density' models (see formula 2 in text)

Species		Intercept	Temperature	Salinity	Oxygen	Turbidity	Temperature²	Salinity²	Oxygen²	Turbidity²	F	R^2
Clupea harengus	b (ß)	3.52	-0.01 (-0.08)	-0.25 (-1.64)	-	-	-	0.005 (1.24)	-	0.06 (0.17)	74	0.33
	t	11.6	-2.2	-8.5	-	-	-	6.5	-	4.3		
Sprattus sprattus	b (ß)	0.03	-0.54 (-1.98)	0.06 (0.26)	0.91 (0.98)	0.55 (0.25)	0.02 (1.37)	-	-0.06 (-1.2)	-	106	0.50
	t	0.03	-10.1	8.0	4.1	6.9	7.4	-	-5.1	-		
Merlangius merlangus	b (ß)	1.45	-	-	-	-1.29 (-1.7)	-	-	-	0.26 (1.33)	149	0.32
	t	18.0	-	-	-	-14.6	-	-	-	11.4		
Trisopterus luscus	b (ß)	-0.78	0.09 (0.49)	-	-	-	-	0.001 (0.14)	-	-	125	0.28
	t	-8.3	14.5	-	-	-	-	4.2	-	-		
Syngnathus rostellatus	b (ß)	-1.09	0.09 (0.54)	0.08 (0.53)	-	-	-	-0.002 (-0.6)	-	-	95	0.30
	t	-4.1	16.3	2.9	-	-	-	-3.2	-	-		
Pomatoschistus microps	b (ß)	4.23	-0.32 (-1.11)	-	-	0.58 (0.25)	0.01 (0.46)	-	-0.01 (-0.2)	-	188	0.55
	t	8.7	-6.2	-	-	7.6	2.7	-	-5.6	-		
Pomatoschistus minutus	b (ß)	-6.81	-0.30 (-0.86)	0.06 (0.18)	1.85 (1.49)	1.55 (0.53)	0.02 (1.43)	-	-0.12 (-1.73)	-0.28 (-0.37)	73	0.45
	t	-3.9	-4.0	5.3	5.0	4.7	7.0	-	-5.8	-3.5		
Pomatoschistus lozanoi	b (ß)	-2.24	0.33 (1.19)	0.30 (1.24)	-	-	-0.01 (-0.97)	-0.01 (-0.96)	-	-	41	0.22
	t	-3.8	5.9	5.9	-	-	-4.8	-4.6	-	-		
Pleuronectes platessa	b (ß)	-0.60	-	0.04 (0.2)	-	0.84 (0.41)	-0.002 (-0.2)	-	-	-	80	0.27
	t	-2.2	-	5.6	-	10.3	-5.2	-	-	-		
Limanda limanda	b (ß)	-10.26	0.36 (1.16)	0.24 (0.8)	1.22 (1.11)	2.68 (1.05)	-0.02 (-1.6)	-0.004 (-0.55)	-0.07 (-1.26)	-0.43 (-0.64)	104	0.58
	t	-8.3	6.3	5.1	4.9	10.3	-9.2	-3.6	-5.6	-6.7		
Platichthys flesus	b (ß)	5.89	-0.03 (-0.18)	-0.17 (-1.2)	-0.47 (-0.85)	-	-	0.002 (0.6)	0.02 (0.75)	-	132	0.51
	t	10.5	-5.1	-7.2	-4.0	-	-	3.7	3.6	-		
Solea solea	b (ß)	5.17	0.15 (0.66)	-0.44 (-2.1)	-	-	-0.003 (-0.35)	0.01 (1.62)	-	-	97	0.37
	t	12.1	3.7	-11.7	-	-	-2.0	9.1	-	-		
Liocarcinus holsatus	b (ß)	1.59	-	-0.33 (-1.78)	-	-	0.004 (0.42)	0.01 (2.25)	0.004 (0.1)	-	202	0.54
	t	5.9	-	-11.8	-	-	13.6	15.1	3.1	-		
Carcinus maenas	b (ß)	-0.53	0.08 (0.3)	0.12 (0.47)	-	-0.49 (-0.22)	-	-	-	-	259	0.54
	t	-1.9	9.4	16.6	-	-6.5	-	-	-	-		
Crangon crangon	b (ß)	0.89	0.09 (0.38)	-	1.23 (1.53)	-	-	-	-0.07 (-1.61)	-	69	0.22
	t	0.9	10.0	-	6.1	-	-	-	-6.5	-		

and turbidity appeared in half of the models. Most of the actual data points fell within the 95 % predictive limits of the models (Fig. 6.5).

Densities for *C. harengus* and *S. sprattus* were predicted to be high at lower temperature and higher turbidity, in a combination with low salinity for *C. harengus*, and with higher salinity and intermediate oxygen levels for *S. sprattus*. Also, whiting densities will be lower in turbid waters. Densities of *T. luscus* and *S. rostellatus* were predicted to increase with increasing temperature at intermediate to high salinity levels. *P. microps* seemed to prefer lower temperature and oxygen values, while turbidity should be higher. *P. minutus* was predicted to have higher densities at moderate oxygen levels, if turbidity and temperature were high and salinity not too low. For *P. lozanoi* higher salinity and temperature seemed to be the forcing variables. High densities for *P. platessa* were predicted with lower temperature and higher turbidity. For *L. limanda* temperature and oxygen should be intermediately low, while turbidity and salinity should be high. *P. flesus* and *S. solea* were predicted to occur at higher densities at lower salinities (and lower oxygen concentrations for *P. flesus*), with a contrasting behaviour towards temperature. High values of salinity and temperature seemed necessary for both *C. maenas* and *L. holsatus*, in combination with low turbidity for *C. maenas* and somewhat higher oxygen levels for *L. holsatus*. Higher densities of *C. crangon* were predicted at moderate oxygen and higher temperature levels.

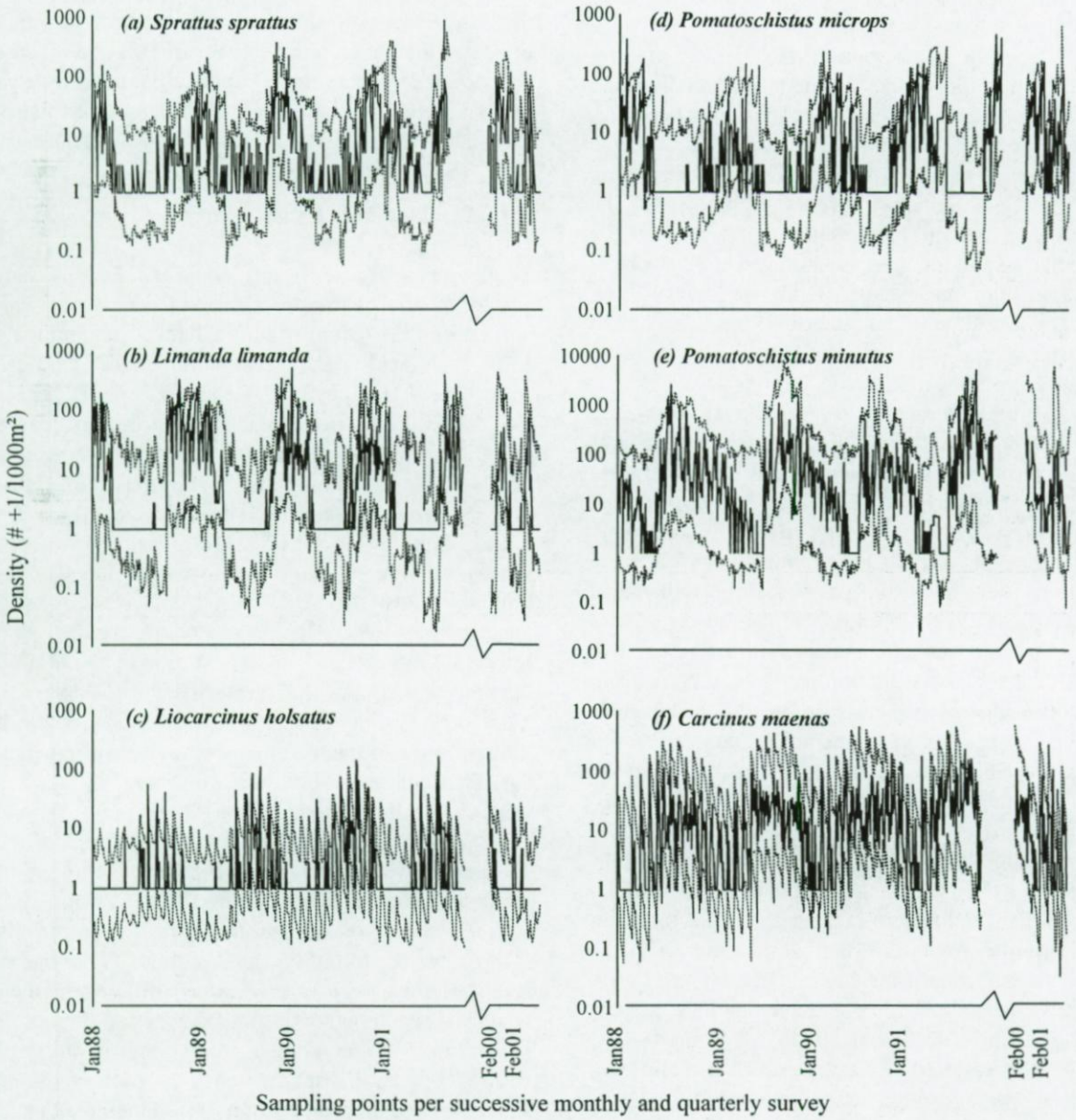

Fig. 6.5 Predictive 95 % confidence limits (broken lines) for six 'density' models and actual density values as individual sampling points (full line), for (a) 1 'marine seasonal', (b-c) 2 'marine juvenile', and (d-f) 3 'estuarine resident' species. Sampling points were ordered from marine to brackish (14 stations) on a monthly basis (48 surveys) between January 1988 and December 1991 and on a quarterly basis (8 surveys) from September 1999 to May 2001

6.4 Discussion

6.4.1 Environmental variables

As the Westerschelde estuary was characterized by a marked gradient in salinity, oxygen and turbidity, these are most likely the factors that will influence the occurrence and density of mobile organisms on a spatial scale. Several studies have shown the importance of a seasonal factor in the distribution of fish and macro-crustaceans, as they only temporarily make use of the estuary as a nursery ground (Hemingway & Elliott 2002). Obviously, temperature is the most suitable variable, although temporal patterns in salinity, oxygen and turbidity were shown as well. Models based on these four (easily monitored) environmental variables are simple, easier to test and cross-validate, and less costly in predicting and controlling the outcome in the future.

The other, extrapolated variables did not contribute significantly to the models. Hydrodynamic variables and sediment characteristics have been recognized as forcing factors on several aspects of the distribution of macrobenthic species (Ysebaert *et al.* 2002). Current velocity was not withdrawn in the models. For fish and macro-crustaceans, currents are indirectly important, mainly during the transport of postlarvae into the estuary (Drake & Arias 1991). The type of sediment was rather uniform (sandy at all 14 stations), and was only determined twice during both survey periods (Chapter 5).

Biotic interactions (*e.g* food availability) are important for the distribution of fish and macro-crustaceans. However, when mysid densities were included, the variance explained only increased slightly (between 0 and 5 %). Moreover, too many sampling points had to be eliminated, which made the models less powerful. Consequently, rather than reflecting causal relationships, the modelled response curves and surfaces should only be seen as descriptions of the actual distribution patterns of the fish and crustacean species in relation to the structuring environmental variables in temperate estuarine environments. Possibly, the combined interaction between the environmental variables is a proxy for prey availability.

Yet, altering the environmental conditions can lead to (drastic) changes in the estuarine populations of fish and macro-crustaceans. Due to major engineering works in the southwest Netherlands, the former Oosterschelde and Grevelingen estuaries were changed into a marine bay and a saline lake, respectively (Nienhuis & Smaal 1994b). For the Oosterschelde, this resulted in a reduced biomass of brown shrimp *Crangon crangon* (Chapter 3). For the Grevelingen, the density of juvenile plaice *Pleuronectes platessa* was reduced with >50% (Doornbos & Twisk 1984), which was only compensated <10% by the increased nursery function of the ebb-tidal delta (Chapter 4-Add.).

In almost all European estuaries, oxygen deficiency has been attributed to excess input of organic matter (Elliott & Hemingway 2002). Oxygen depletion highly restricted the distribution of fish and crustaceans in the upper part of the Schelde estuary till the mid 1990s (Van Damme *et al.* 1994, Mees *et al.* 1993a). Although, water quality improved in this part of the estuary, densities of the commonest species are still very low (Maes *et al.* 1998a). Synergistic interactions between reduced oxygen levels and increased water temperatures, *e.g* through cooling water discharges from power plants, may also occur (Cattrijsse *et al.* 2002).

Physical disturbances, such as dredging and relocation of sediments, may increase turbidity. Although, turbidity is important in lowering predation pressure, extreme values provide a direct negative effect on the health and behavior of fish and macro-crustaceans, not only on recruitment but possibly also on the gill function and respiration of fishes (Marchand 1993, Elliott & Hemingway 2002).

6.4.2 Single-species response curves

Single species response curves were relatively successful to predict the probability of occurrence, and agreed with the real distribution, habitat requirements and ecological tolerances found in literature (Cattrijsse & Hampel 2000, Froese & Pauly 2002).

Estuarine dependent species are considered to be eurytopic, with a high tolerance towards a broad range of environmental conditions. For *Crangon crangon* no significant response curves were found, even by converting low densities into absences or by converting real densities into discontinuous density-classes instead of binary presence/absence data. This is related to the fact that brown shrimp was present almost always and at high numbers throughout the Westerschelde (Chapter 2). Most other species are likely to be found within a limited range of one or more of the 4 environmental variables, although this does not mean the species were physically limited to these ranges.

Within the taxonomic groupings, none of the species showed a comparable preference in all 4 variables. The response curves for the 2 clupeoids (*Clupea harengus* and *Sprattus sprattus*) were only comparable for turbidity; the 2 gadoids (*Trisopterus luscus* and *Merlangius merlangus*) differed in their response to temperature and oxygen; the 3 gobiids (*Pomatoschistus minutus*, *P. lozanoi* and *P. microps*) showed opposite responses in all variables; *Solea solea* showed opposite responses than the other 3 flatfish species to all variables, *Platichthys flesus* to salinity and oxygen, *Pleuronectes platessa* and *Limanda limanda* to turbidity; the 2 crab species (*Car-*

cinus maenas and *Liocarcinus holsatus*) differed in their oxygen preference.

On the other hand, several species responded the same way to the four environmental variables, if compared per ecological guild. The 15 species were classified as 6 estuarine resident species, 2 marine seasonal (or adventitious) species and 7 marine juvenile species (Table 6.1). Four marine juveniles (whiting, bib, sole and flying crab) were more likely to be found at higher temperatures, higher salinities and lower turbidities, while the opposite holds true for 2 estuarine resident species (common goby and flounder). Three estuarine resident species (Nilsson's pipefish, sandgoby and shorecrab) showed similar response curves as the marine juveniles. This is related to the fact that most marine juveniles enter the estuary during springtime and only stay for a relatively short period, which was also the case for the latter 3 (so-called) estuarine residents in the Westerschelde (Chapter 2). Three marine juveniles (herring, plaice and dab) and a marine seasonal species (sprat) rather responded like estuarine residents to temperature and turbidity. In contrast to the other marine juveniles, the latter 4 species arrived at a later moment to winter, and were present during most of the year (except dab) in the Westerschelde (Chapter 2).

6.4.3 Presence/Absence models

The final presence/absence models and their validations achieved similar results, and the standard deviations on the validation diagnostics were very small. This suggested that the regressions were independent of the chosen set of actual observations. For the 8 most common species the sensitivity was higher than the specificity, which means that their presence in the Westerschelde was better predicted than their absence.

Temperature seemed to be an important forcing factor in the presence/absence models as well. This indicated that the prediction of occurrence was mainly dependent on a temporal effect. But the presence/absence models also showed that different environmental variables interact both at temporal and spatial scales. For example, the response curves for *Pleuronectes platessa* and *Pomatoschistus minutus* showed a positive relation with increasing salinities, although it has been shown that flatfish and gobies were more common in the 'brackish water' reaches of the Westerschelde (Chapter 2). Actually, they have a higher probability to be found during the colder months when the saltwedge penetrates deep into the middle reaches of the estuary (Fig. 6.3). The interaction between low temperatures and higher salinities became clear from the negative sign of the regression coefficient for temperature and the positive sign for salinity (Table 6.3).

Little information is found on tolerance for suspended material (or turbidity) by fishes in European estuaries (Cattrijsse 1997). In the Humber estuary (UK) the same correlations for fishes were found with temperature, salinity and dissolved oxygen concentration, but not with turbidity (Marshall & Elliott 1998). Probably, this is one of the first studies to show that several fish and crustaceans have a preference for a limited part of the turbidity range. For *Pomatoschistus lozanoi* this was the only significant response curve in relation to the separate environmental variables. The spatial effect of turbidity was found to significantly contribute to the predictive success of 8 presence/absence models, mainly for species with a higher probability of occurrence at higher turbidities.

Dissolved oxygen concentration was of minor importance in the presence/absence predictions, and the relation with the ecological guilds was less obvious. Fish and crustaceans are highly mobile and can easily avoid low oxygen levels (Elliott & Hemingway 2002). In the lower part of the Schelde estuary, some species were found even at oxygen levels to 2 $mg.l^{-1}$ (Maes *et al.* 1998b). During the study period, dissolved oxygen concentration was never a limiting factor, as it dropped below 5 $mg.l^{-1}$ only once in the Westerschelde.

6.4.4 Density Models

Understanding the nature of possible interactions between variables is necessary to improve the understanding of changes in estuarine fish communities (Power *et al.* 2000b). The density models generally failed to predict extreme peaks and troughs, which is not uncommon to data series that fluctuate through several orders of magnitude (Nisbet & Gurney 1982). Still, most models agreed with the actual distribution of the species, as a vast majority of the sampling points fell within the 95% predictive confidence limits of the models. Only seven models could explain more than 45 % of the variance. No better models were built when only part of the data (*e.g* the monthly data from 1988-1991) was used. The simplicity of the models inevitably incorporated some loss of certainty as probably not all relevant forcing factors have been taken into account.

Fish and macro-invertebrate populations are characterized by high inter-annual variability (see previous chapters). The year-class strength is determined at the early-life history stages through a mechanism that is not yet well understood (see Costa *et al.* 2002). However, water temperature seems to be a key factor affecting the year-class variability. Low winter temperatures are favourable for several fish species (*e.g.* Pihl 1990, see Chapter 4), while mild winter temperatures are preferred by several macro-invertebrates (see Chapter 5).

Habitat complexity and habitat quality have been shown to be important for the distribution of fish and macro-crustaceans in estuaries (Elliott &

Hemingway 2002), but as such, these parameters could not be entered in the models. Food is probably a major factor determining habitat quality (Gibson 1994). However, if food is not a limiting factor (see Chapter 7 and Chapter 8), then temperature is likely to be the most important factor controlling growth (Gibson 1994). Also, the extent of predation might be important to describe habitat quality, but few studies have quantitatively examined predation (in relation to habitat complexity) in different habitats (Costa *et al.* 2002).

The final density models predicted both temporal and spatial patterns, in accordance with the presence/absence models. However, the withdrawn variables per species were not necessarily similar between both types of models. The standardized regression coefficients for temperature and salinity (or their quadratic effects) were highest in 5 and 6 models, respectively. Additionally, higher densities for 8 species were predicted with increasing salinities in the Westerschelde, all or not in combination with lower temperatures. Also in the Humber estuary (UK), salinity was the dominant factor influencing the fish distribution (Marshall & Elliott 1998). This is in contrast with the findings in the inner Severn (UK) and Elbe (Germany) estuaries, where pronounced annual cycles in species composition occurred irrespective of seasonal changes in salinity (Potter *et al.* 1997, Thiel & Potter 2001). Most probably this difference was related to the higher number (and density) of diadromous fish species present in the 2 latter systems.

Turbidity and dissolved oxygen concentration were entered as the first variable in 2 models each. In Australian and South African estuaries, the relation between turbidity and fish distribution was much more pronounced (Blaber 1997). Dissolved oxygen concentration was withdrawn in 7 density models, but only in combination with most other effects. This was probably due to the fact that the seasonal pattern in dissolved oxygen concentration was largely opposite to temperature. However, it seemed to be an important variable in the prediction of *Crangon crangon* densities, comparable with the models built for the shrimp population from the Thames estuary (Attrill *et al.* 1999).

Density estimates were better for most of the estuarine resident species, and least for most of the marine juvenile species. Best models were built for those species that were present in the estuary for a longer period, but with only one clear density peak in either a cold or a warmer season. This was independent of whether (shorecrab, common goby, sprat and flounder) or not (dab, flying crab and sandgoby) they were present in the estuary throughout the year (Hostens *et al.* 1996). The combined interaction between the four environmental variables was the main forcing factor behind the temporal and spatial distribution of these seven species. The lowest R^2 values were allocated to species that either were present in the estuary during only a short period (*e.g* bib, whiting and nilsson's pipefish), or to species with higher densities in both a warmer and a colder season (*e.g* sole, herring, plaice, lozano's goby and brown shrimp) (Chapter 2). Most probably, the temporal and spatial distribution of the latter eight species was more governed by the proper appearance of suitable food resources (Hemingway & Elliott 2002).

In a next step, the robustness of the models will be tested, by applying them to presence/absence and density data from other marine ecosystems, such as the Oosterschelde marine bay (Chapter 4, Chapter 5) and the Humber estuary (Marshall & Elliott 1998). Also, other models like the PISCES model by Henderson & Seaby (1994) or the ones generated for the Thames estuary (Attrill *et al.* 1999), will be applied to the fish and macro-crustacean data from the Westerschelde estuary.

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CHAPTER 6 - ADDENDUM APPLICATION OF THE WESTERSCHELDE RESPONSE MODELS TO FISH AND MACRO-CRUSTACEAN DATA FROM THE OOSTERSCHELDE

K. Hostens

Abstract. The aim of this study is to test the applicability of the statistical models, which were developed to predict fish and macro-crustacean responses to the environmental conditions in the Westerschelde estuary (Chapter 6). For this, a data set from the Oosterschelde was used. The probability of occurrence and the prediction of abundance of several dermersal fish and macro-crustaceans in reponse to four environmental variables (salinity, temperature, dissolved oxygen concentration and turbidity) are investigated. The present study can only be seen as a preliminary attempt to validate the robustness of the models that were established for another system. The diagnostics (% correctly predicted, sensitivity and specificity) for the 15 presence/absence models based on the Oosterschelde data were comparable to the diagnostics based on the Westerschelde data. Only the models that explained >45 % of the variance in density for six species in the Westerschelde, were applied to the density data from the Oosterschelde. These were largely successful when temperature was the main forcing variable (e.g. for Sprattus sprattus and Pomatoschistus microps). The constant high salinity in the Oosterschelde is a favorable condition for Carcinus maenas and Liocarcinus holsatus, partially masking the effect of the other environmental variables in these models. Limanda limanda and Pomatoschistus minutus have different seasonal distribution patterns in both systems. In the Westerschelde both species only occurred during a relatively short period, while in the Oosterschelde they were present throughout the year. This shows the difficulty of applying statistical models from a real estuary to a different type of ecosystem, namely a marine bay like the Oosterschelde.

6.1 Introduction

Changes in the environment can affect the distribution of several organisms (*e.g* Kröncke 1990, Pihl & van der Veer 1992). For example, alteration of the Oosterschelde estuary (NL) into a marine bay, lead to an increase in the biomass of flatfish and gadoids, but shrimp biomass was found to have decreased shortly after the engineering works were completed (Chapter 3). On the other hand, ten years after the closure of the former Grevelingen estuary (NL), the density and biomass of O-group plaice were reduced with more than 50 % (Doornbos 1982). Next to the fact that postlarvae could hardly enter the Grevelingen system anymore, this reduction was probably related to the continuous oligo-mesotrophic conditions in the saline lake.

Estuarine environments are important nurseries for juvenile fish and macro-crustaceans (see Elliott & Hemingway 2002). To be able to manage these systems from an ecological point of view, it is necessary to understand the relationship between the biota and the environment. The demersal fish and macro-crustacean assemblages in shallow estuaries and coastal areas are mainly structured by salinity, temperature and exposure/habitat type (*e.g.* Chapter 2-Add.2). It may be desirable to be able to predict the responses of fish and macro-crustaceans to (changes in) these environmental variables, in order to predict the effects of human interventions.

Up till now a number of studies developed predictive models for different taxonomic groups in single systems (*e.g.* Attrill *et al.* 1999, Ysebaert *et al.* 2002), but none of these tried (or were able) to validate their models with data from other ecosystems. However, validation of the robustness of statistical models is a prerequisite for them to be useful.

In a previous study, predictive models of the occurrence and density for a number of demersal fish and macro-crustaceans in response to a limited set of environmental variables in the Westerschelde estuary were established (Chapter 6). In the present study a first attempt is made to externally validate these response surfaces with data from the adjacent Oosterschelde marine bay.

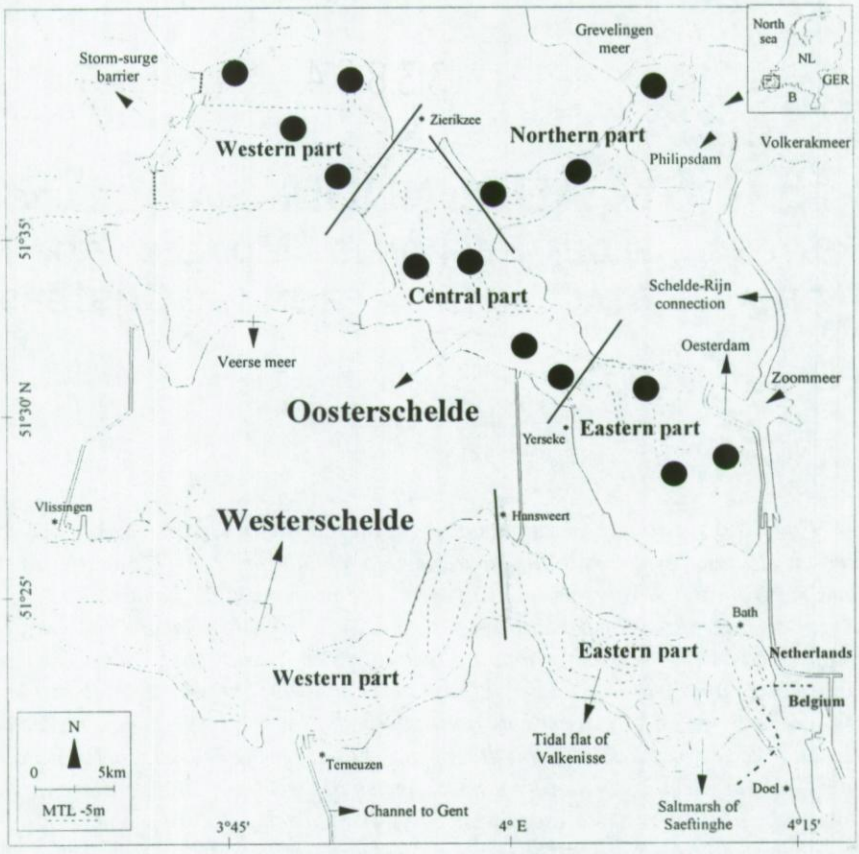

Fig. 6.6 Map of the Oosterschelde and Westerschelde with indication of the 14 stations sampled in the Oosterschelde

6.2 Material and methods

The Oosterschelde is located north of the Westerschelde estuary and is connected with it indirectly through sluices and canals (Fig. 6.6). Through major engineering works in the period 1960-'87, the Oosterschelde was altered from a true estuary into a marine bay. As a consequence, the major estuarine gradients in salinity, turbidity and oxygen concentration have disappeared. Details on the geomorphology, hydrodynamics and ecology are given in Nienhuis & Smaal (1994a).

Only for a limited part of the large Oosterschelde data set on demersal fish and macro-invertebrates, the environmental variables were recorded simultaneously (see Chapter 1). Data were taken from 8 surveys conducted at 14 subtidal stations in the Oosterschelde (Fig. 6.6). The demersal fish and macro-invertebrate fauna was sampled with a 3-m beam trawl on a quarterly basis between September 1999 and May 2001. A total of 112 sampling points could be used. See Chapter 4 and Chapter 5 for details on the sampling and data processing.

Based on a large data set from the Westerschelde, presence/absence and density models for 12 fish and 3 macro-crustacean species were developed (Chapter 6). For a description of the methodology, the selection of the species, and the model diagnostics and parameters, the reader is referred to that paper. The environmental variables used were salinity (psu), temperature (°C), dissolved oxygen concentration (mg l^{-1}) and turbidity (as the reciprocal of secchi depth, m^{-1}). See Chapter 5 and Chavatte (2001), for the patterns in these environmental variables.

The final model equations (based on multiple logistic regressions), which predict the occurrence of fish and macro-crustaceans in the Westerschelde, were applied to the Oosterschelde data. The predictive success, sensitivity (% presence predicted as being present) and specificity (% absent predicted as being absent) were calculated.

Also, the final multiple (lognormal) regressions, which predict the abundance of the fish and macro-crustaceans in the Westerschelde, were externally validated with the same data from the Oosterschelde. Only the models that explained >45 % of the variance in the Westerschelde (6 models, *Platichthys flesus* was excluded as this species is almost absent from the Oosterschelde), were used. For these models it was shown that the combined interaction between the four environmental variables was the main forcing factor behind the temporal and spatial distribution of the seven species, rather than the proper appearance of suitable food resources (Chapter 6). The predicted values were graphically compared with the real density data, but not statistically tested.

Table 6.5 Validation of the 15 final presence/absence models, established for the Westerschelde, with the Oosterschelde data: predictive success (% correct), specificity (% absent predicted as absent) and sensitivity (% present predicted as present)

Species	Oosterschelde		
	%corr	%AasA	%PasP
Clupea harengus	69	80	28
Sprattus sprattus	76	82	63
Merlangius merlangus	42	49	32
Trisopterus luscus	66	70	61
Syngnathus rostellatus	49	64	17
Pomatoschistus microps	72	80	55
Pomatoschistus minutus	86	11	92
Pomatoschistus lozanoi	66	76	41
Pleuronectes platessa	83	29	91
Limanda limanda	76	46	85
Platichthys flesus	55	72	28
Solea solea	74	79	67
Liocarcinus holsatus	69	58	76
Carcinus maenas	88	-	92
Crangon crangon	96	-	98

6.3 Results

The coefficients for the different presence/absence and density models are given in Chapter 6.

The final logistic models from the Westerschelde were able to predict the presence of the most common species in the Oosterschelde (Table 6.5). For 9 out of 15 species >70 % of the occurrences were correctly predicted. Only the prediction for *Merlangius merlangus* and *Syngnathus rostellatus* failed in >50 %. Sensitivity was <40 % for four species, with the least successful prediction of presences for *S. rostellatus* and *Platichthys flesus*. Specificity was relatively high, although the absence of six species could not be predicted very well. For *Pomatoschistus minutus* and *Pleuronectes platessa* <30 % of the absences were predicted to be absent, and for the most common macro-crustaceans *Crangon crangon* and *Carcinus maenas* in the Oosterschelde the prediction of absence failed.

The prediction of the density for six species in the Oosterschelde based on the final density models from the Westerschelde was less successful. The models were able to predict the major pattern for *Sprattus sprattus* and *Pomatoschistus microps*, and to a lesser extent for *Liocarcinus holsatus* and *Carcinus maenas* (Fig. 6.7). For *Limanda limanda* the autumn and winter densities could be predicted fairly well (at least the major patterns), but the model failed to predict spring and summer densities. The opposite holds for the density model for *Pomatoschistus minutus*, where autumn and winter densities were not predicted very well.

6.4 Discussion

Fish and macro-crustaceans belong to the higher trophic levels and are present in a variety of trophic chains. They can be indicators of the changes occurring in other components of the ecosystem such as plankton and benthos (Marchand *et al.* 2002). As fish and macro-crustaceans (like crabs and shrimps) may be commercially exploited, the general public may be more attentive to information about these components. As such, they can be important indicator species and it may be interesting to know how species respond to changes in the environment, and if these responses can be predicted.

Statistical models are best validated with data from other ecosystems. For the fish and macro-

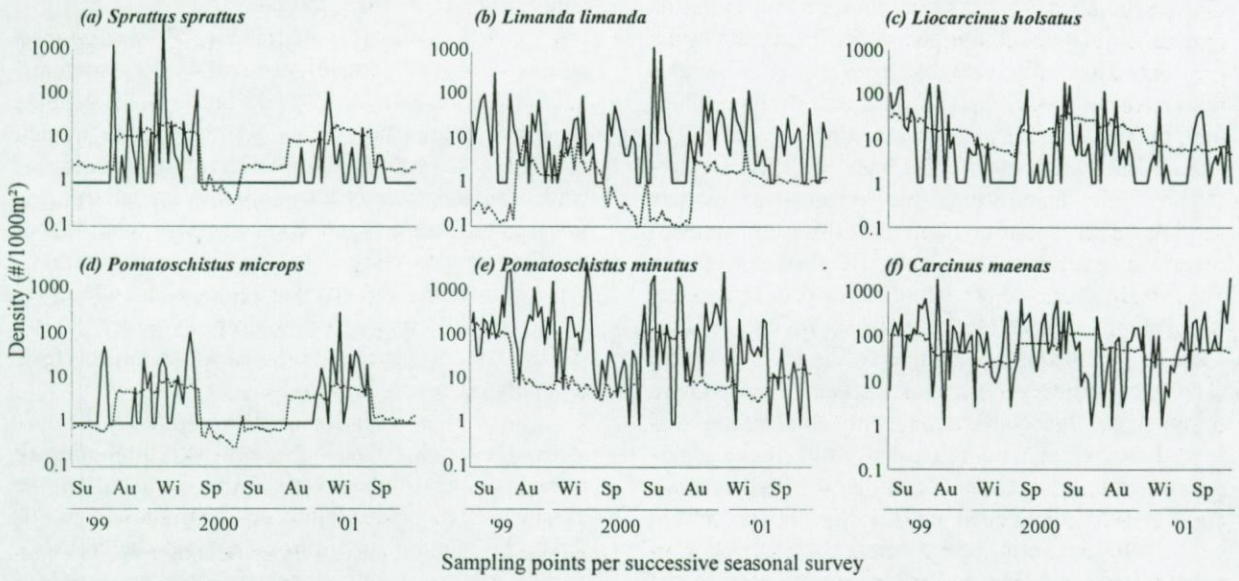

Fig. 6.7 Predicted (broken line) versus actual (solid line) density values in the Oosterschelde, based on the final density models from the Westerschelde for 4 fish species (a-b, d-e) and 2 crustacean species (c, f). Sampling points were ordered from west to east (12 stations) for 8 successive seasons from summer 1999 to spring 2001

crustaceans large data sets exist for both the Westerschelde and the Oosterschelde, sampled in a uniform way (see Chapter 1). Although, the Oosterschelde is an estuary *s.l.* according to Day *et al.* (1989), it is hardly recognized as such according to the definition *s.s.* given by Pritchard (1967). Important estuarine gradients (salinity, oxygen, turbidity) in the Oosterschelde have disappeared (Nienhuis & Smaal 1994b). However, as for now, this is the best external data set from an adjacent system available. Another problem is the fact that only for a limited part of the Oosterschelde data set, environmental variables were simultaneously measured. Furtheron, almost no data exist on sediment characteristics from the sampling points. A discussion on the importance of food, prey-availability and predation as structuring factors, and the reasons why these factors were not included in the models, were given in Chapter 6.

Salinity, temperature, oxygen and turbidity are important structuring factors in the fish assemblage (Chapter 2-Add.2). Still, it was shown that most species have a broad tolerance towards changes in the environment, as they are able to thrive under typical estuarine conditions (Chapter 6). However, the average density of macro-crustaceans was at least twice as high in the Westerschelde as in the Oosterschelde, and the average density of all fish species together was highest in the brackish reaches of the Westerschelde (Chapter 2-Add.2). On the other hand, there is a clear seasonal pattern with a succession of species and life-stages, clearly correlated with changes in the four environmental variables that were used in the models (Hostens *et al.* 1996, Chapter 4, Chapter 5).

Salinity has long been regarded as the most important structuring factor for estuarine biota that show strong seasonal patterns (Attrill *et al.* 1999). As the Oosterschelde was altered into a marine bay, a number of species (*e.g. Syngnathus rostellatus*, *Platichthys flesus*) are not common (anymore) in this system (Chapter 4). On the other hand, estuarine resident species like *Crangon crangon* and *Carcinus maenas* are present in the Oosterschelde throughout the year (Chapter 5). This makes it not very useful to model the responses of these species in the Oosterschelde. The least-fitting presence/absence models were those where salinity and turbidity were the main factors in explaining the response surfaces for the Westerschelde or where temperature played an inferior role (*e.g. Merlangius merlangus*, *Liocarcinus holsatus*, *Pleuronectes platessa*). Although, typical estuarine gradients in the Oosterschelde environment disappeared, seasonal changes in temperature, dissolved oxygen concentration and turbity were apparent (Chapter 5). It is concluded that the logistic models that were developed for the Westerschelde, are capable of predicting the (temporal) occurrence of several demersal fish and macro-crustaceans in the adjacent Oosterschelde.

The study from the Westerschelde already showed that it is rather difficult to predict abundance of demersal fish and macro-crustaceans. Only for species governed mainly by a combined interaction between the four environmental variables, the models were acceptable. The density models established for eight species from the Westerschelde, which were not used here, had a low explanatory value for the Westerschelde data themselves (see Chapter 6 for a discussion). This makes them less suitable to apply to data from other systems. The models presented by Attrill *et al.* (1999) for *Crangon crangon* and *Carcinus maenas* from the Thames estuary (UK), included an instrumental binary variable (indicating presence/absence per month) to capture seasonality. However, by constraining the models with 12 binary variables a huge amount of the variation was eliminated, which increased the R^2 values but not necessarily made the models fit better to the real data.

Application of the Westerschelde density models to the Oosterschelde ecosystem was only partly successful. The relative success for the crab species (*Carcinus maenas* and *Liocarcinus holsatus*) could be attributed to the fact that the Oosterschelde complied with the higher salinity preference of these species. The seasonal pattern was fine-tuned through temperature (higher densities at higher temperatures) as the second important effect. The appearance of high densities of postlarvae of both crab species in spring (related to an increasing temperature) indicated the importance of the system for these species (Chavatte 2001).

The best-fitted models were for those species with a clear seasonal appearance in the system. Both *Sprattus sprattus* and *Pomatoschistus microps* were absent during the spring-summer (warmer) period. Higher densities were indeed predicted during winter and the colder autumn seasons. For those species the effect of the other variables is inferior to the effect of temperature as the main forcing variable.

The density pattern for *Pomatoschistus minutus* was comparable between the two systems, but the autumn and winter peaks in the Oosterschelde were not predicted with the Westerschelde model. Sand gobies were predicted to have higher densities with increasing temperature, slightly higher salinity, lower dissolved oxygen concentrations and higher turbidity in the Westerschelde. The first conditions were fulfilled but oxygen was rather high and turbidity in the Oosterschelde seldom exceeded 1 m^{-1} (Chapter 5). The prediction failed as the latter effects probably got too much weight.

In the Westerschelde *Limanda limanda* showed a peculiar density pattern with total absence in spring and summer, which was predicted by the Westerschelde model. However, dab showed a different distribution pattern in the Oosterschelde. Also, in the surfzone of Belgian beaches dab was only sporadically recorded between September and October (Beyst *et al.* 2001), but in the shallow ebb-tidal delta

of the Grevelingen (NL) dab was present thoughout the year (Chapter 4-Add., K. Hostens unpublished data). In the period 1969–'78, before the engineering works in the Oosterschelde, dab showed more or less the same density pattern as in the Westerschelde (De Veen *et al.* 1979). As the Oosterschelde was altered from a real estuary into a marine bay, the density pattern of *L. limanda* resembled the coastal pattern, where small juveniles arrived earlier at higher densities and especially larger individuals (1 and 2 group) stayed longer in the Oosterschelde ecosystem during springtime (Chapter 4).

If the Oosterschelde were still a real estuary, then probably the models would have fit much better. The present study proved the difficulty of applying density models to different types of ecosystems.

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CHAPTER 7 THE MYSID-FEEDING GUILD OF DEMERSAL FISHES IN THE BRACKISH ZONE OF THE WESTERSCHELDE ESTUARY

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Key words: stomach content, consumption, Mysidacea, flatfish, gobies, gadoids, clupeoids

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Abstract. *The demersal fish fauna of the mesohaline zone of the Westerschelde estuary (south-west Netherlands) was sampled intensively in the period 1990-1992. Almost 500 beam trawl samples were taken in both subtidal (330 samples) and intertidal (144 samples) habitats. These yielded 44 fish species, mostly as juveniles. The area was found to function as a nursery for several demersal fish species. and harboured large populations of hyperbenthic mysids. Three gobies, three flatfish, one clupeoid and one gadoid dominated the fish fauna, while three mysid species were important components of the holohyperbenthos. From c. 1500 stomach contents of 25 fish species, 44 prey species were identified, the most abundant of which were also common in the hyperbenthal. The demersal fish community consisted of a group that foraged subtidally on fast-moving epi- and hyperbenthic prey (for example gadoids, gobies and clupeoids) and a group that foraged on slow-moving or sessile endobenthic organisms, mainly in intertidal areas (for example most flatfish species). Mysidacea occurred in >50 % stomachs analysed and were taken as prey by 19 of the 25 fish species. Mysids were most important in the diets of Pomatoschistus minutus, P. lozanoi, Trisopterus luscus and Merlangius merlangus, and were present in appreciable numbers in Pleuronectes flesus, Trigla lucerna, Clupea harengus and Pleuronectes platessa. These species fed mainly on the brackish water endemic Neomysis integer. Mesopodopsis slabberi (present in 35 % of the gobiid stomachs) and Gastrosaccus spinifer (present in 25 % of the gadoid stomachs) were of secondary importance. P. minutus and T. luscus showed a diet shift from calanoids (Eurytemora affinis and Temora longicornis) to mysids at L_S of 30 mm and 50 mm, respectively. Only 1 % of the standing stocks of the N. integer and M. slabberi populations (as measured at the moment of sampling) was removed per day by the local demersal fish community, so top-down control of mysid populations in estuaries seems unlikely.*

7.1 Introduction

Lumping of taxonomically often very different species into trophic guilds (groups of species or size classes of species that share similar preys) has become an important tool in reducing the complexity of ecosystems for the description of local food webs (Elliott & Dewailly 1995). Recent studies suggest that, although the species composition of the fish fauna can differ significantly between estuaries, similar feeding guilds can be distinguished over wide geographical ranges (Costa & Elliott 1991).

Most estuarine fish species are known to be opportunistic feeders, although their diet is more or less restricted to part of the total available prey spectrum as dictated by their capability to capture and ingest specific prey species. Therefore, most dietary shifts (ontogenetic, seasonal, or shifts towards the most profitable prey) are related to *e.g* the trophic adaptability of the fish species, food partitioning and/or seasonality in the availability of preys (Gerking 1994).

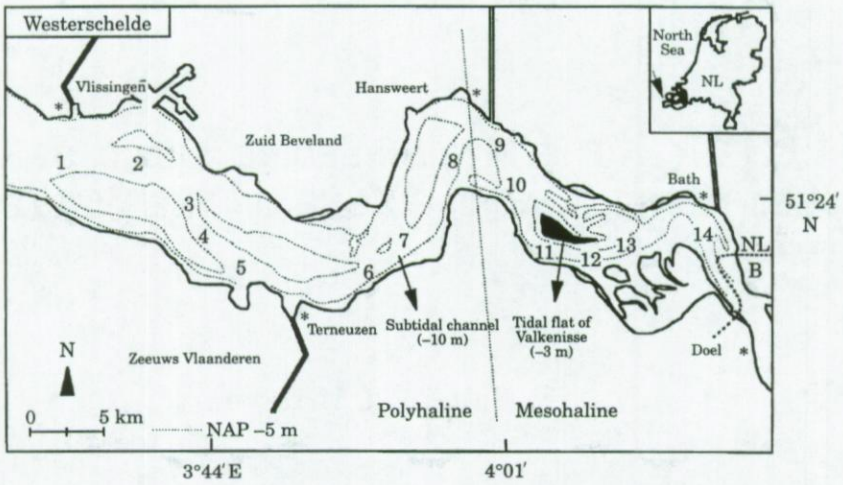

Fig. 7.1 Map of the study area with location of the 14 stations in the subtidal channel and of the intertidal flat of Valkenisse

In the mesohaline subtidal zone of the Westerschelde estuary (average salinity for the study period: 19.1 ± 3.6 psu) the hyperbenthos reaches maximal densities (Mees *et al.* 1993b, Mees *et al.* 1995), while almost no macro-endobenthic organisms occur (cf. burial and clogging of the feeding apparatus in highly turbid areas). A hyperbenthos-feeding guild has been distinguished recently in several studies of demersal fish assemblages (*e.g* Moreira *et al.* 1992). The hyperbenthos mainly consists of peracarid crustaceans and larvae of a variety of taxa, and several endobenthic species perform regular excursions into the hyperbenthic layer (Mees & Jones 1997). Mysidacea, the most typical hyperbenthic taxon, occur abundantly in estuaries where they are an important component in the diet of several fish species (Mauchline 1980). The size of estuarine mysids (mm) is intermediate between that of mesozooplanktonic (µm) and endo- or epibenthic (cm) prey items, and often they replace copepods progressively in the diet of post-larval and juvenile fish (Sorbe 1981). The presence of an estuarine mysid-feeding guild of demersal fishes in the Westerschelde was investigated by means of stomach analyses of representative length classes of all fish species that utilise both intertidal and subtidal habitats in different seasons. Correlations between the stomach content data and the availability of different mysid species in different seasons and habitats are discussed.

7.2 Materials and methods

The Westerschelde estuary is the lower part of the river Schelde and is located in the so-called Delta area in the south of the Netherlands (Fig. 7.1). It is characterized by a marked salinity gradient and a virtually completely mixed water column. The residence time of the water is about 60 days or 120 tidal cycles in the mesohaline zone (Soetaert & Herman 1995b). Salinity zones in the estuary remain relatively stable and are maintained in more or less the same position throughout a tidal cycle (Heip 1989b). The major part of the estuary is characterized by two parallel subtidal channels separated by large sandflats and bordered by tidal mudflats and marshes (Van Maldegem *et al.* 1993). The abiotic environment is discussed in Heip (1989b) and Van Eck *et al.* (1991).

Demersal fishes were sampled with 3 and 2-m beam trawls equipped with fine-meshed nets (5 x 5 mm) and a tickler chain. From January 1990 to December 1991, monthly samples were taken subtidally (-10 m depth) in 14 stations between Vlissingen and Bath. Concurrently, the hyperbenthos was sampled with a sledge equipped with nets with a 1-mm mesh size. Details of the sampling methodology and results for the hyperbenthic compartment are given in Mees *et al.* (1993a), Mees *et al.* (1993b) and Mees *et al.* (1994). From March to October 1992, the intertidal sandflat of Valkenisse was sampled monthly at depths of -1 m and -3 m. Trawling was always carried out with the tide at an average speed of 4.5 knots relative to the bottom and over a distance of 1000 m. All fish and mysids were identified to species level, measured and counted. Fish were anaesthetised with benzocaine to prevent regurgitation of the stomach contents and preserved in a 7 % formaldehyde-seawater solution. Densities were standardized as numbers of individuals per 1000 m². More details on the spatial and temporal community structure of the epibenthos are given in Chapter 2-Add.1 and Chapter 2; data on the fauna of the intertidal sandflat are presented in Hostens *et al.* (1996).

Based on the local and seasonal patterns in the species composition and on the length-frequency distributions of the dominant species, 1486 individuals belonging to 25 fish species (mostly O- or 1-group individuals) were selected for stomach content

analysis. All prey items were identified to the highest taxonomic separation possible. The diet composition is summarized as the numerical percentage of the main prey taxa per fish species and as frequency of occurrence for the mysid species. A more detailed description of the diet composition per size class is given for those fish species where mysids were found to be a major component in the diet. The minimal number of mysids consumed, was estimated by multiplying the average number of mysids per stomach by the number of fish present per unit area. This was done for each fish species and for each month separately. The consumption of mysids by the entire demersal fish community of the brackish zone of the Westerschelde estuary was then estimated as the sum of the consumption estimates for all fish species, expressed as number removed from the standing stocks of three mysid species (as measured at the moment of sampling) per 1000 m^2 per day.

7.3 Results

7.3.1 Demersal fish community

From the 45 epibenthic species caught, only a few fish and crustacean species were abundant or common in the Westerschelde. For several species, the mesohaline zone (stations 9-14) was characterized by higher densities than the polyhaline zone (stations 1-8) (Fig. 7.2). This was especially the case for the one shrimp species: brown shrimp *Crangon crangon* (L.); for three goby species: sand goby *Pomatoschistus minutus* (L.), Lozano's goby *P. lozanoi* (de Buen) and common goby *P. microps* (Krøyer); and for the flatfish species plaice *Pleuronectes platessa* (L.), flounder *P. flesus* (L.), sole *Solea solea* (L.) and dab *Limanda limanda* (L.). Crabs, both shore crab *Carcinus maenas* (L.) and swimming crab *Liocarcinus holsatus* (Fabricius) were more important in the polyhaline zone (stations 1-8). Other important fish groups in the mesohaline zone were gadoids, mainly bib *Trisopterus luscus* (L.) and whiting *Merlangius merlangus* (L.), and clupeoids, mainly sprat *Sprattus sprattus* (L.) and herring *Clupea harengus* (L.).

7.3.2 Stomach analyses

Of the 1486 stomachs analysed, 491 stomachs were empty, mainly from plaice, dab, flounder, sprat and sandeel *Ammodytes tobianus* (L.) (all sampled subtidally) and from intertidally sampled sole (Table 7.1). An average of two different prey species were found per stomach, though some individuals had a more diverse diet (>5 prey species consumed). An average of 14 prey items per stomach was recorded but, if calanoids are excluded, this value is reduced to 6. Some fish species had very high numbers of prey items per stomach (*e.g* up to 200 in some individuals of sprat).

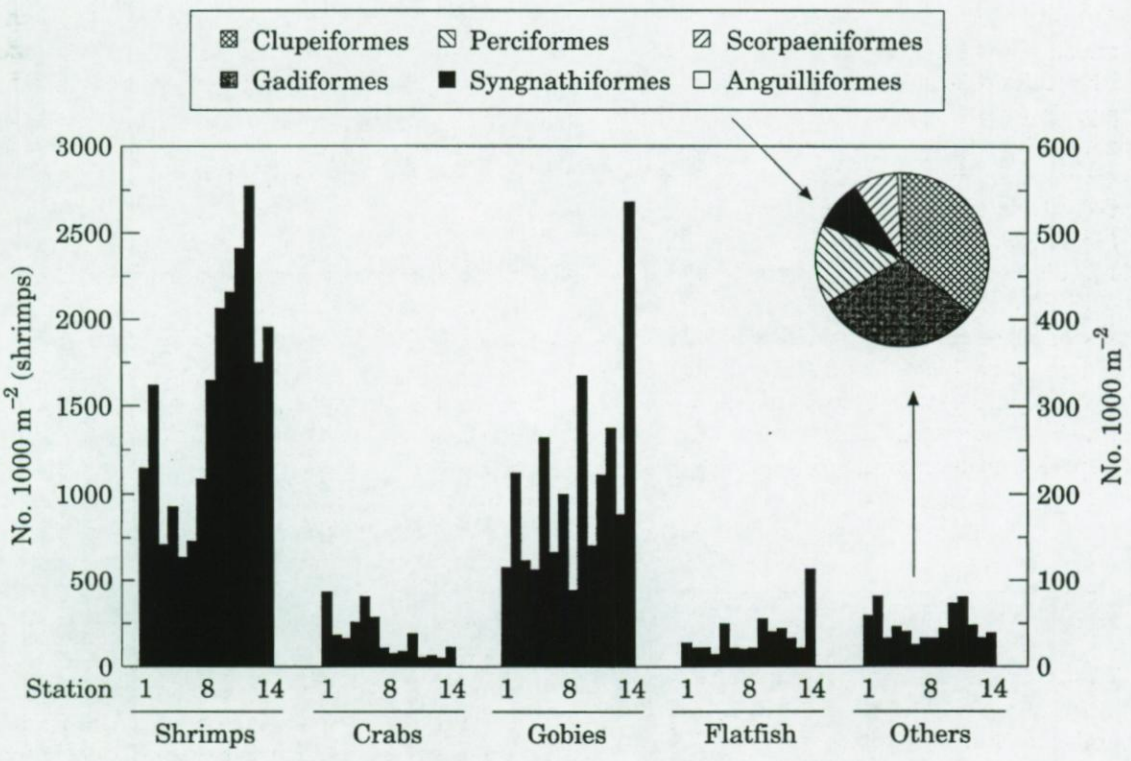

Fig. 7.2 Average density along the salinity gradient per taxonomic group (period 1990-1991, for station numbers see Fig. 7.1, left axis only for shrimp), and the relative numerical composition of the group of other fishes (pie chart)

Table 7.1 Numbers of stomachs analysed of the 25 fish species, with minimal and maximal L_S, average numbers of prey species and prey items per stomach, relative numerical diet composition for the important prey groups, and frequency of occurrence of the five mysid species; all individuals caught subtidally, unless indicated otherwise

Fish Species	L_S (mm)		Stomachs		Average prey per stomach			Relative numerical diet composition†									Frequency of occurrence‡				
	Min	Max	Total	Empty	No. spp.	No. items	No. items*	N.-Mala.	Mysid.	Amphi.	Carid.	O.Crus.	Teleo.	Mollu.	Polyc.	Others	*Neo int*	*Mes sla*	*Gas spi*	*Sch spi*	*Sch ker*
Clupea harengus	58	109	30	9	2	45	7	84	14	0·3	0·3	—	0·1	—	1	—	62	—	—	—	—
Sprattus sprattus	58	133	68	48	2	201	1	100	0·1	—	—	0·1	—	—	—	—	10	—	5	—	—
Gadus morhua	48	483	4	—	2	5	5	—	10	—	38	29	14	—	5	—	—	—	25	—	—
Merlangius merlangus	45	237	38	1	2	21	11	47	41	1	7	0·3	3	—	0·1	0·1	19	3	41	8	3
Trisopterus luscus	30	225	132	6	3	17	17	2	78	4	11	1	1	—	0·4	—	57	1	24	1	1
Ciliata mustela	63	203	31	2	2	8	8	—	8	24	51	3	5	—	2	—	14	—	3	—	3
Dicentrarchus labrax	38	193	9	—	3	21	11	49	21	11	8	—	—	—	7	—	22	—	11	—	11
Liparis liparis	26	71	30	1	2	9	7	17	14	49	19	—	0·4	—	0·4	0·4	31	—	3	3	—
Ammodytes tobianus	64	176	51	44	3	29	3	91	—	—	—	1	—	—	3	2	—	—	—	—	—
Hyperoplus lanceolatus	181	186	2	2	—	—	—														
Callionymus lyra	94	103	3	1	2	2	2	—	—	25	50	25	—	—	—	—	—	—	—	—	—
Pomatoschistus microps	23	54	52	3	2	11	3	75	3	4	0·2	0·2	—	—	1	17	16	2	—	—	—
Pomatoschistus minutus	19	67	284	25	2	5	3	43	34	14	1	1	0·1	—	1	6	59	34	2	—	0·4
Pomatoschistus lozanoi	23	54	236	21	2	3	2	28	55	15	1	0·4	0·1	—	0·3	—	57	43	3	0·5	0·5
Pleuronectes platessa (intertidal)	13	119	34	1	3	47	26	45	2	9	2	0·1	—	7	20	15	21	—	—	—	3
Pleuronectes platessa	49	248	134	106	1	1	1	—	70	—	—	—	—	18	9	—	4	—	7	—	—
Limanda limanda	53	273	123	102	1	2	2	—	—	—	6	3	—	86	—	—	—	—	—	—	—
Pleuronectes flesus (intertidal)	170	360	30	4	1	12	12	—	32	58	6	0·3	2	1	—	—	35	—	—	—	—
Pleuronectes flesus	79	362	102	86	1	6	6	—	1	7	12	—	3	73	2	—	—	—	6	—	—
Solea solea (intertidal)	64	286	49	18	2	8	7	3	1	68	18	2	—	—	7	—	3	—	3	—	—
Anguilla anguilla	235	650	21	4	1	5	5	—	—	31	14	11	43	1	—	—	—	—	—	—	—
Belone belone	129	129	1	—	2	9	8	11	89	—	—	—	—	—	—	—	—	100	—	—	—
Gasterosteus aculeatus	50	67	3	3	—	—	—														
Trigla lucerna	126	249	8	2	2	14	14	—	54	—	45	1	—	—	—	—	33	—	—	—	—
Myoxocephalus scorpius	114	214	3	—	2	2	2	—	—	—	57	14	29	—	—	—	—	—	—	—	—
Enophrys bubalis	81	153	2	—	2	2	2	—	—	—	33	—	33	—	—	—	—	—	—	—	—
Agonus cataphractus	66	138	6	2	2	4	4	13	13	50	19	—	—	—	—	—	25	—	25	—	—
25			1486	491	2	14	6	54	24	8	5	1	1	2	3	3	42	18	7	1	1

*Average number of items without Non-Malacostraca.
†Non-Malacostraca, Mysidacea, Amphipoda, Caridea, Other Crustacea (Brachyura, Isopoda), Teleostei, Mollusca, Polychaeta, Others (Detritus, Ctenophora).
‡*Neomysis integer*, *Mesopodopsis slabberi*, *Gastrosaccus spinifer*, *Schistomysis spiritus*, *Schistomysis kervillei*.

Besides some unidentifiable material and faecal pellets, 44 different prey species were recorded (Table 7.2). Only 13 species were very abundant: palps of polychaetes (probably from the capitellid *Heteromastus filiformis* (Claparède)), siphons of bivalves (probably exclusively from *Macoma baltica* (L.)), the calanoid copepods *Eurytemora affinis* (Poppe) and *Temora longicornis* (Müller), the gammaridean amphipods *Corophium volutator* (Pallas), *Gammarus salinus* (Spooner) and *Bathyporeia* species, the mysids *Neomysis integer* (Leach), *Gastrosaccus spinifer* (Goës) and *Mesopodopsis slabberi* (van Beneden), different developmental stages of *Crangon crangon*, postlarval gobies (different *Pomatoschistus* species) and postlarval clupeoids (probably a mixture of *Clupea harengus* and *Sprattus sprattus*).

Mysids were found in more than half of the stomachs and they were taken by 19 fish species (Table 7.1). They dominated (>50 %) the diet of subtidally sampled bib, lozano's goby, plaice, tub gurnard *Trigla lucerna* (L.) and garfish *Belone belone* (L.). They were subdominant (between 10 and 50 %) in the diets of herring, whiting, seabass *Dicentrarchus labrax* (L.), sea snail *Liparis liparis* (L.), sand goby, flounder (intertidally caught), and hooknose *Agonus cataphractus* (L.). No mysids were recorded from the stomachs of sandeel, dragonet *Callionymus lyra* (L.), dab, eel *Anguilla anguilla* (L.), bull rout *Myoxocephalus scorpius* (L.) and sea scorpion *Enophrys bubalis* (Euphrasen). The calanoids *E. affinis* and *T. longicornis* were numerically important prey for several species, especially for the two clu-

Table 7.2 Overview of all 44 prey species identified in the stomach content analyses of the 25 fish species, with the total number of prey items found in all stomachs per prey group and per prey species

Prey Group	Total	Prey species	No.	Remarks
Polychaeta	387	Polychaeta spp.	12	
		Heteromastus filiformes	268	Mostly palps, probably exclusively from this species
		Nereis virens	41	Often recorded as Nereidae spp.
		Eteone longa	31	
		Lanice conchilega	5	Also Aulophora larvae
		Pygospio elegans	4	
		Spiophanes spp.	4	
		Anaitides spp.	2	
Mollusca	211	***Macoma baltica***	119	Mostly siphons, probably this species
		Ensis spp.	88	
		Spisula spp.	3	Spat
		Littorina spp.	1	Single record
Non-Malacostraca	7481	*Daphnia magna*	556	Recorded in only 1 stomach
		Daphnia pulex	12	Recorded in only 1 stomach
		Copepoda spp.	1625	
		Eurytemora affinis	3866	
		Temora longicornis	1102	
		Acartia spp.	154	
		Centropagus hamatus	4	
		Paracalanus parvus	1	Single record
		Euterpina acutifrons	140	
		Cirripedia spp.	20	Only cypris Larvae
Amhipoda	1145	***Corophium volutator***	452	Often recorded as *Corophium* spp.
		Gammarus salinus	321	
		***Bathyporeia* spp.**	330	
		Corophium arenarium	34	
		Pontocrates altamarinus	3	
		Jassa falcata	2	
		Pleusymtes glaber	2	
		Parajassa pelagica	1	Single record
Isopoda	14	*Lekanosphaera rugicauda*	11	
		Idotea linearis	3	
Mysidacea	3350	***Neomysis integer***	1875	Marsupial larvae separated
		Gastrosaccus spinifer	1115	Idem
		Mesopodopsis slabberi	324	
		Schistomysis kervillei	27	Idem
		Schistomysis spiritus	9	
Caridea	659	***Crangon crangon***	659	Zoeae, postlarvae and juveniles
Brachyura	42	*Carcinus maenas*	24	
		Liocarcinus holsatus	11	
		Portumnus latipes	5	
		Liocarcinus arcuatus	2	
Teleostei	111	Pisces species	7	
		***Pomatoschistus* spp.**	72	
		***Clupeidae* spp.**	31	
		Ammodytes tobianus	1	Single record
Others		Ctenophora spp.	1	Single record
		Faecal pellets		
		Unidentifiable material		
	13 400	44		

Table 7.3 Number of stomachs analysed and relative numerical diet composition per length class for two goby species

Fish L_S (mm)	19–21	22–24	25–27	28–30	31–33	34–36	37–39	40–42	43–45	46–48	49–51	52–54	55–57	58–60	61–63	67–69
Pomatoschistus minutus																
No. stomachs	2	2	4	7	7	17	45	37	58	60	23	8	3	7	2	1
Calanoidea	100	82	97	50	35	17	4	22	28	21	71	58	37	59	0	100
Mysidacea	0	18	1	27	6	46	68	50	46	44	22	22	0	21	60	0
Amphipoda	0	0	1	0	9	32	25	25	14	24	7	5	11	15	20	0
Others	0	0	1	23	49	5	3	3	12	11	0	15	53	5	20	0
Pomatoschistus lozanoi																
No. stomachs		1	1	15	29	43	53	47	31	9	4	3				
Calanoidea		0	50	13	10	27	21	3	51	41	29	67				
Mysidacea		100	50	76	71	61	56	70	36	46	57	33				
Amphipoda		0	0	8	17	12	22	24	11	14	7	0				
Others		0	0	3	2	0	1	3	2	0	7	0				

peoids herring and sprat, for whiting and for most perciforms. The amphipod *C. volutator* was important in sole and in intertidally caught flounder, while *G. salinus* and *Bathyporeia* species were important in the diets of sea-snail and gobies, respectively.

The shrimp *C. crangon* was most important in the diets of the gadoids, especially five-bearded rockling *Ciliata mustela* (L.) and cod *Gadus morhua* (L.), in dragonet and in the scorpaeniform fish species, *e.g* tub gurnard and hooknose. Bivalve siphons were mainly taken by older flatfishes from the subtidal area and by juvenile plaice intertidally, while fragments of teleost fish were found mainly in the stomachs of older eel, bull rout, cod, rockling and whiting. Palps of capitellid polychaetes were recorded from intertidal plaice, and segmented fragments of several polychaete species were taken by sole, plaice, seabass and sandeel. Unidentifiable prey fragments and faecal pellets were most abundant in common goby and intertidal plaice.

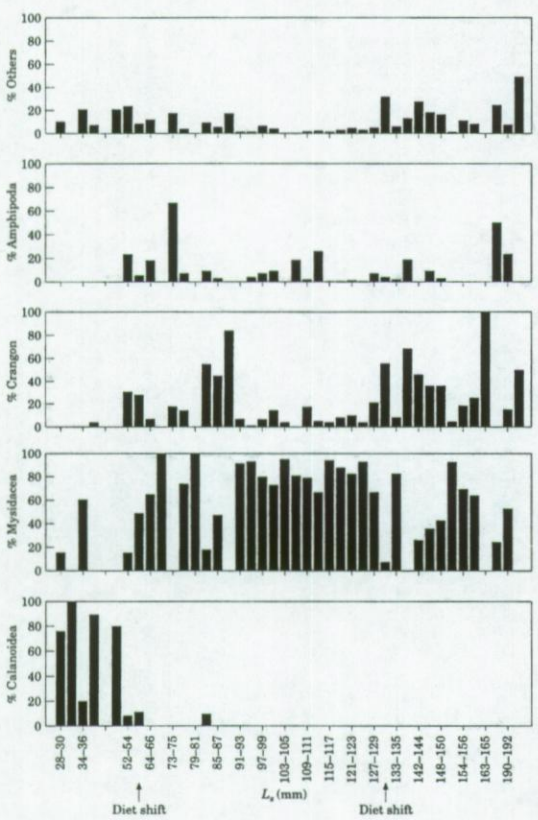

Fig. 7.3 Relative numerical diet composition for *Trisopterus luscus* per length class

7.3.3 Niche shift

The stomach contents of 284 *Pomatoschistus minutus* between 19 and 67 mm, 236 *P. lozanoi* between 23 and 54 mm, and 126 *Trisopterus luscus* between 30 and 210 mm L_S were analysed. For both gobies, calanoids were numerically important prey items (Table 7.3). They were the dominant prey item for several length classes of sand goby (<30 and >50 mm). Between 30 and 50 mm the species mainly preyed upon mysids, while they supplemented their diet with amphipods. Lozano's goby seems to be a mysid feeder throughout its life, though amphipods and calanoids became more important in the diet of medium-sized and larger individuals, respectively (Table 7.3). Bib showed a clear diet shift from calanoids to mysids at a length of 50 mm (Fig. 7.3). A second shift from mysids to shrimp was observed at a length of 130 mm. These larger size classes also fed to a large extent on mysids, but the strictly hyperbenthic *Neomysis integer* has more or less been replaced by the larger, epibenthic *Gastrosaccus spinifer*.

7.3.4 Consumption of mysids

Neomysis integer was preyed upon by 15 fish species. It occurred in >50 % of the stomachs of bib, sandgoby, lozano's goby and herring (Table 7.1). *Mesopodopsis slabberi* occurred in 30 and 40 % of the stomachs of sandgoby and lozano's goby, respectively. *Gastrosaccus spinifer* was mainly taken by bib, whiting and cod. *Schistomysis spiritus* and *S. kervillei* were less important, although they were

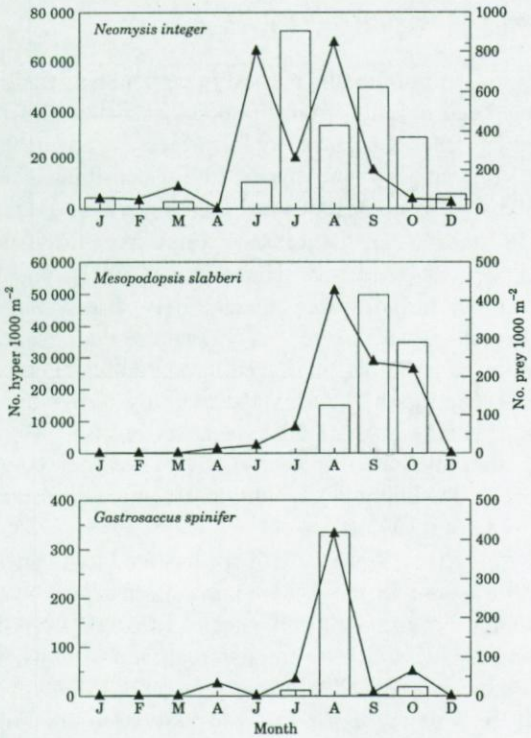

Fig. 7.4 Monthly density pattern of three mysid species as caught with a hyperbenthic sledge (left axis, line) (Mees *et al.* 1993a, Mees *et al.* 1994), in comparison with the recalculated number of consumed mysids by all 25 fish species caught with a 3-m beam trawl (right axis, bars), in the mesohaline part of the Westerschelde

recorded from stomachs of seabass and whiting, for example.

Only small fractions of the standing stock of the *N. integer* and *M. slabberi* populations were consumed per day by all demersal fish species together. For example, maximally 800 out of 80000 *N. integer* and 400 out of 50000 *M. slabberi* per 1000m² were taken by fish in July and September, respectively (Fig. 7.4). The seasonal consumption pattern followed the density pattern of the prey population for both *N. integer* and *M. slabberi*. A single peak of 400 individuals per 1000m² was observed for *Gastrosaccus spinifer* in summer, while about the same number of individuals was found to be consumed per day by the fish community.

7.4 Discussion

7.4.1 General

The structural pattern found in the mobile epibenthic fauna of the Westerschelde estuary in the period 1990-1991 is comparable with the results for 1988 and 1989 (Chapter 2-Add.2, Chapter 2). These studies described a clear separation between a polyhaline (stations 1 to 8) and a mesohaline (stations 9 to 14) zone, the latter being characterized by higher densities of both invertebrates and fishes. The mobile epibenthic fauna is dominated by invertebrate species in both zones: the shrimp *Crangon crangon* occurred in much higher densities than all fish species together. Also for other compartments like the hyperbenthos and the zooplankton, the mesohaline zone is characterized by much higher densities and biomasses (*e.g* Mees *et al.* 1993b, Soetaert & Van Rijswijk 1993, Chapter 8-Add.).

Most of the 44 fish species were recorded in low average densities (34 species with <1 individual per 1000m²). The few abundant species were caught mainly as juveniles, especially in the mesohaline zone. The Westerschelde is, therefore, considered to be a nursery area for 8 fish species: *Pomatoschistus minutus*, *P. lozanoi*, *P. microps*, *Limanda limanda*, *Pleuronectes platessa*, *Trisopterus luscus*, *Sprattus sprattus* and *Solea solea*. For this study, the diet of these species was investigated. Further, stomach contents were analysed for all other fish species that were found to be locally and/or seasonally abundant, i.e. *Clupea harengus*, *Liparis liparis*, *Pleuronectes flesus*, *Ammodytes tobianus*, *Ciliata mustela*, *Merlangius merlangus*, *Anguilla anguilla*, *Dicentrarchus labrax*, and for some rarer species (*Trigla lucerna, Agonus cataphractus, Gadus morhua, Callionymus lyra, Myoxocephalus scorpius, Enophrys bubalis, Hyperoplus lanceolatus* and *Belone belone*).

7.4.2 Habitat use

Stomach contents were analysed from fishes taken from both subtidal and intertidal areas. Although this is not presented in the results section, the species may be divided clearly into three groups according to their foraging strategy. A first group utilizes only the subtidal reaches (*e.g* gadoids and clupeoids) where they prey mainly upon mobile hyper- and epibenthic species. A second group (*e.g* flatfishes) forages mainly intertidally, taking sessile or buried endobenthic prey. A third group of species (*e.g* gobies) did not show a clear preference, feeding in both subtidal and intertidal areas.

Similar feeding patterns have been observed in other areas. In the lower Medway estuary (UK), for example, the gadoids *Trisopterus luscus* and *Merlangius merlangus* predominantly fed on fast-moving brown shrimp, mysids and small fish, while pleuronectids preferred tubificid and polychaete worms (van den Broek 1978). In the western Irish Sea, 13 fish species were divided into a group that preyed predominantly on mobile prey organisms such as decapods, mysids, copepods and fish, and a second group that exploited mainly in/epifaunal organisms such as polychaetes, bivalves and echinoderms (McDermott & Fives 1995). In the present study area, only 20 % of 134 juvenile plaice sampled subtidally had full stomachs and had consumed mainly mysids (*Gastrosaccus spinifer* and *Neomysis inte-*

ger), bivalves (*Ensis* spp.) and polychaetes (*Nephtys* spp.). These were almost certainly taken in intertidal areas. Plaice that were sampled intertidally invariably had full stomachs. They had mainly cropped bivalve siphons, most probably from *Macoma baltica* which is the most abundant bivalve species on the sandflat of Valkenisse (Ysebaert *et al.* 1993). Also, >80 % of 102 flounder stomachs from the subtidal areas were empty. On the intertidal flat, most stomachs were full and their diet consisted mainly of *Corophium* species and, to a lesser extent, mysids. Sole has also been reported to perform tidal migrations. The high percentage of empty stomachs, even on the intertidal flat, probably reflects a nocturnal feeding behaviour (Boerema 1964). The stomachs of juvenile dab in the subtidal areas were nearly always empty. This suggests that dab uses mainly the estuary as a wintering area where they survive on their fat-reserves.

7.4.3 Diet composition

As in most estuarine systems, the immigration or appearance of early life-history stages of most fish species in the mesohaline zone of the Westerschelde coincides with peak densities of the dominant copepod species *Eurytemora affinis* (Soetaert & Van Rijswijk 1993). Several fish species then show a diet shift: as the fish grow, mysids replace copepods progressively in the diet. This was clearly the case for 30-mm *Pomatoschistus minutus*, which can be related to a transition from a planktonic to a demersal life style (R.V. Arellano et al. unpublished data). In the Po River Delta (Italy), sea bass also shifted preference from copepods towards mysids at a length of 30 mm (Ferrari & Chieregato 1981). In the Westerschelde, mysids were an important prey item for both sandgoby and lozano's goby. In Belgian coastal waters, *Pomatoschistus minutus* preyed mainly upon parts of sessile organisms, such as polychaete radioles, bivalve siphons and amphipods (Hamerlynck & Cattrijsse 1994) while the sympatric *P. lozanoi* preyed mainly upon mysids, small shrimps, amphipods and early postlarval fish (Hamerlynck *et al.* 1990). It can be argued that in coastal areas, where mysids are less abundant than in estuaries (Mees *et al.* 1993a), feeding niches are spatially segregated through interspecific competition, with *P. minutus* feeding closer to the bottom than *P. lozanoi*. In the brackish water zone of estuaries, where food is unlikely to be a limiting factor since hyperbenthic densities are high throughout the year, both species prefer to feed on mysids. The diets of the gadoids *Trisopterus luscus* and *Merlangius merlangus* shifted from calanoids to mysids and amphipods, and then to shrimps and small fishes, as has also been observed in other studies (*e.g* Chapter 7-Add.). Still, mysids are clearly more important in the diet of estuarine bib populations than for bib in coastal areas.

7.4.4 The mysid-feeding guild

In Europe, the highest hyperbenthic densities have been reported from the brackish reaches of estuaries (Mees *et al.* 1993b, Mees *et al.* 1995). Throughout the year, hyperbenthic densities in the polyhaline zone of the Westerschelde are on average 5-10 times lower than those reported from the mesohaline zone (Mees & Hamerlynck 1992). In the maximum turbidity zone, the numbers of sessile macrobenthic organisms generally decrease due to burial and/or clogging of their feeding apparatus (Pearson & Rosenberg 1987). Also, the mobility of hyperbenthic species can be an advantage, for example allowing an immediate response to adverse oxygen conditions in the unpredictable environment of an estuary (Mees *et al.* 1993b).

Many demersal fish species feed to a considerable extent in the hyperbenthic part of the water column. From the 44 prey species recorded from the stomachs, 35 species were also recorded from hyperbenthos samples taken in the same area (Mees *et al.* 1993b, Mees *et al.* 1995). Most of these are holohyperbenthic taxa (*e.g* mysids and gammaridean amphipods), while others belong to the merohyperbenthos (*e.g* larval shrimps, crabs and fish) or to the mesozooplankton that happens to be present in the water layers close to the substratum (*e.g* the calanoid copepods). Also, taxa that are generally described as endobenthic are known to perform regular excursions into the water column (examples are macrobenthic Amphipoda and meiobenthic Harpacticoida: see Mees & Jones (1997) for a review). These temporary hyperbenthic individuals, although they constitute a small fraction of the total endobenthic population, are obviously more vulnerable to fish predation.

Mysidacea are probably the most typical hyperbenthic taxon (Mauchline 1980, Mees & Jones 1997). In a review on the occurrence of mysids in the diet of fish, Mauchline (1980) reports 51 and 12 fish species that feed on mysids in the Northeast Atlantic and the Mediterranean, respectively. Since that time, mysid-feeding guilds have been distinguished in several demersal fish assemblages (Mees & Jones 1997). In the intertidal mudflats of the upper Tagus estuary (Portugal), for example, the group of mysid-eaters included *Dicentrarchus labrax*, two *Pomatoschistus* spp. and three *Syngnathus* spp. (Moreira *et al.* 1992). Based on the diet of 17 fish species from the Cananeia estuary (Brazil), Ribeiro *et al.* (1997) distinguished four feeding groups, with one group that mainly fed on suprabenthic mysids and copepods. Burke (1995) suggested that the estuarine gradient in mysid densities might influence the movement of southern flounder *Paralichthys lethostigma* (Jordan and Gilbert) to their nursery grounds.

In the Westerschelde, the two most abundant mysid species are *Neomysis integer* and *Mesopodopsis slabberi*. Both species reached average densities

of >10 individuals per m^2 in the mesohaline subtidal zone (Mees *et al.* 1993a). It is obvious that mainly these two species were preyed upon by the different fish species. *N. integer* is a typical endemic of brackish waters and it is very abundant in both the subtidal channels and intertidal saltmarsh creeks (Mees *et al.* 1993a). Peak densities of >100 individuals per m^2 in the subtidal were noted in summer (Mees *et al.* 1994). *M. slabberi* is very abundant in fully marine and in brackish waters. In the Westerschelde, it enters the mesohaline zone mainly in the summer period, where it occurs generally somewhat higher in the hyperbenthal layer, as compared to *N. integer*. The occurrence of *Gastrosaccus spinifer* is correlated with sediment characteristics and seems to be independent of salinity (Mees *et al.* 1993a). The low densities of *G. spinifer* estimated from the subtidal sledge samples (Fig. 7.4) are probably severe underestimates as the species buries itself in the sand of shallow areas. The second peak of mysids in the diet of *Trisopterus luscus* (>140 mm L_S) consisted mainly of *G. spinifer*. The three other mysid species of the Westerschelde were preyed upon only rarely in the Westerschelde. *Praunus flexuosus* (Müller) is essentially an intertidal species that is probably too large a prey item for juvenile fishes. Both *Schistomysis spiritus* (Norman) and *S. kervillei* (G.O. Sars) are more marine species that do not penetrate far into the estuary (Mees *et al.* 1993a). While juvenile *T. luscus* fed mainly upon *N. integer* in the Westerschelde, *S. kervillei* was the most important mysid species in its diet in an adjacent coastal area (Chapter 7-Add.).

This study confirms that the hyperbenthos, and mysids in particular, are important in the diet of O-group individuals of several fish species in the mesohaline zone of the Westerschelde estuary. Only a small fraction of the mysid populations, however, seems to be consumed by the demersal fish community (on average 1 % of the standing stock of mysids per day). Of course this has to be seen as a minimal consumption estimate. In this study it is assumed that the stomach content represents a feeding period of 24 hours. Several studies indicated a cyclical food intake by different fish species with bursts of feeding either related with light (more feeding at dawn and dusk or during day or night) or related with the tides (more feeding around high water). Other studies showed the opposite, where fish species feed till they are saturated and start feeding again when the stomach is emptied (see Elliott *et al.* 2002). Mysids are known to concentrate near the bottom at high current velocities (J. Mees, pers. comm.). As such they may be more vulnerable to predation between high and low water, when the highest current velocities occur (*i.e.* 4 times a day). Therefore, we suggest that a maximal consumption estimate of 4 % of the standing stock of mysids per day (indicating the fish have been feeding 4 times the amount that was found at a certain sampling moment, per day throughout the year) would be more appropriate.

Still, this is only a rough estimate, as consumption estimates should take into account daily rations and gastric evacuation rates of the different fish species on the one hand and secondary production rather than standing stock values on the other. The present study only intended to give a basic idea of what amount of the mysid population was consumed. Even the 4 % estimate provides an argument against top-down control mechanisms as major driving forces of invertebrate population structures in estuaries. Preliminary results indicate that the highly abundant shrimp *Crangon crangon* may be the most important predator on mysids (Chapter 8).

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CHAPTER 7 - ADDENDUM GROWTH, FEEDING, PRODUCTION, AND CONSUMPTION IN O-GROUP BIB (*TRISOPTERUS LUSCUS* L.) AND WHITING (*MERLANGIUS MERLANGUS* L.) IN A SHALLOW COASTAL AREA OF THE SOUTH-WEST NETHERLANDS

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Key words: North Sea, trophodynamics, daily ration, production, consumption, O-group gadoids, *Trisopterus luscus*, *Merlangius merlangus*, conversion efficiency

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Abstract. *In 1988 juvenile bib (Trisopterus luscus) and whiting (Merlangius merlangus) were studied in a shallow coastal area by monthly sampling with fine-meshed nets. O-group fish of both species are first caught in May. By the end of the first growth season bib reached about 150 mm SL (standard length), whiting about 170 mm SL. Maximal densities were recorded in June and by the end of the year most fish had left the area. The instantaneous mortality is estimated at 0.008 day^{-1} (0.77 % day^{-1} for bib and 0.76 % day^{-1} for whiting) for both species. In May both species depended almost exclusively on calanoid copepods. In June and July mysids and amphipods were the most important invertebrate prey, but small fishes such as gobies provided a substantial proportion of the energy requirements, especially in whiting. From August onwards shrimp and fish dominated the diet in both species. Using Jones' (1974) model, food consumption as per cent body weight day^{-1} varied between 4 and 6 % during summer and declined to 2 to 3 % in autumn. Total consumption per unit area of subtidal seafloor, by the O-group fish of both species taken together, was estimated at 0.47 g ash-free dry weight (ADW) m^{-2} year^{-1} using Jones' (1974) model and at 0.57 g ADW m^{-2} year^{-1} using a conversion efficiency (P:C ratio) of 0.34.*

7.1 Introduction

O-group bib *Trisopterus luscus* and whiting *Merlangius merlangus* are an important ecological component of estuaries (Claridge & Potter 1984), marine bays (Chapter 3), and shallow coastal areas (Redant 1977). Bib are not landed in great quantities in the North Sea but are commercially important in France (Desmarchelier 1985b), Portugal (Sobral & Rebordão 1982), and Spain (Benvegnú 1971). Whiting are of considerable commercial importance (Hislop & MacKenzie 1976) and rank second in weight terms in groundfish surveys in the central, southern, and eastern North Sea (Daan *et al.* 1990).

Data on the food of larval bib and whiting, to a size of 11 mm, in the southern North Sea are given in Last (1978). Information on the food of bib of less than 130 mm is needed, but cannot be obtained from commercial catches (Santos 1989). Some data exist on the food of O-group bib in the Irish Sea (Nagabhushanam 1965, Armstrong 1982), the Loire estuary (Robin & Marchand 1986), the Medway (van den Broek 1978), and the Elbe (Kühl 1973). There is

also some "grey" literature on the subject (*e.g* Gherbi-Barre 1983, Puente 1986). For O-group whiting there are data from Icelandic waters (Pálsson 1980), the Scottish west coast (Gordon 1977b), the Irish Sea (Nagabhushanam 1965), the northern North Sea (Robb & Hislop 1980, Robb 1981), and the Medway estuary (van den Broek 1978). A very extensive report on the food of whiting in the North Sea is given in Hislop *et al.* (1991), but the smallest size class covered in that study is 100 to 149 mm total length. This size class corresponds to O-group only for the last quarter of the year.

In order to fill the gap in the knowledge on food consumption by bib and whiting, O-group fish were collected using fine-meshed nets in a shallow coastal nursery area during 1988.

7.2 Material and methods

7.2.1 Study area

The study area proper covers the central part of the Voordelta (Fig. 7.5a) which is the shallow coastal area formed by the interlinked ebb-tidal deltas of the (former) estuaries of the Dutch Delta where three main European rivers, the Rhine, the Meuse, and the Schelde, enter the North Sea. The Voordelta stretches from the Belgian-Dutch border in the south to the Hoek van Holland in the north. Its marine boundary is arbitrarily defined by the depth contour of 10 m below mean tidal level (MTL), as defined for Amsterdam, which is at 10 to 15 km seaward from the coastline. A detailed description of the hydrodynamics and geomorphology of the Voordelta is given in Louters *et al.* (1991).

The area was greatly affected by the engineering works which were undertaken to protect Zeeland from disastrous storm surges (Louters *et al.* 1991). In relation to these engineering works the benthic ecology of the area has been quite extensively studied: meiofauna (Heip *et al.* 1990, Vanreusel 1990, Vanreusel 1991), macrofauna (Craeymeersch *et al.* 1990) and hyperbenthos (Hamerlynck & Mees 1991, Mees & Hamerlynck 1992).

The spatial structure of the fish and mobile epifaunal assemblages in the area is discussed in Chapter 2-Add.2). The area is a nursery for flatfish, especially dab, sole, and plaice (Chapter 4-Add.). Data on the parasites of juvenile gadoids in the area will be published elsewhere (van Damme *et al.* 1996).

7.2.2 Sampling

During 1988 monthly samples were taken at 24 stations in the Voordelta (Fig. 7.5a). These stations cover two depth strata (5 m below MTL and 10 m

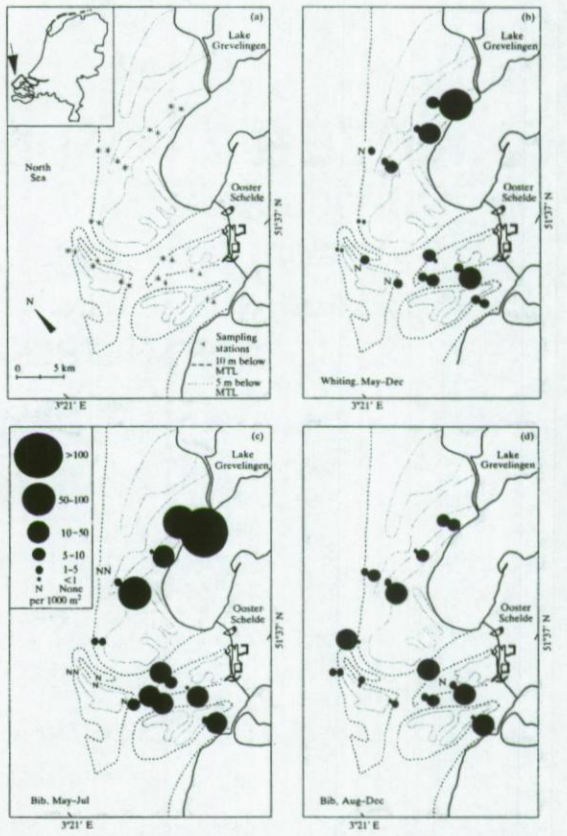

Fig. 7.5 Map of the study area: (a) sampling stations, (b) distribution of whiting mean densities, (c) distribution of bib mean densities from May through July, (d) distribution of bib mean densities from August through December. MTL is the mean tidal level as defined for Amsterdam

below MTL) at 12 localities. Samples were taken from the RV "Luctor" (34 m, 500 Hp) using a 3-m beam trawl, equipped with a 6-m long shrimp net with a 5x5 mm mesh in the cod-end, a tickler chain, and a chain in the groundrope. Hauls were 1 km in length, starting from a buoy or other fixed marker, the distance covered being read from the radar screen. Ship speed relative to the bottom when trawling was about 4.5 knots.

All bib and whiting were anaesthetized in a benzocaine solution in seawater to avoid unnecessary suffering and to prevent regurgitation of the stomach content, and were preserved in 7% neutralized formalin. For gadoids of over 70 mm the abdominal cavity was opened to allow rapid fixation of stomach contents. Standard length (SL), which is a more accurate measure than total length (TL), *e.g* in case of fin lesions, was recorded for all fish specimens. As in fisheries research, TL is the most commonly used measure linear regressions were calculated between SL and TL for a size range of both species. When comparing the results from the present study with studies using TL, the TL measurements were first converted to SL. Biomass was calculated from length-ashfree dry weight (ADW) regressions. Ash-free dry weight (ADW) was measured as the difference between

dried (60°C for 5 days) and ashed (550°C for 2 h) weights of a size range of both species.

Net efficiency, the number of O-group gadoids caught in comparison to the number actually present per fished unit area of subtidal seabed, was assumed to be 20 % for all size classes of fish. This point is taken up in the Discussion. Densities were calculated as N 10^{-3} m^{-2}, biomass as gADW 10^{-3} m^{-2}. For conversion to numbers caught 10^{-3} m^{-2}, densities have to be divided by five. For conversion to numbers caught h^{-1} of trawling no exact factor can be given. Although the hauls were 1 km in length, haul duration depended on current velocity, wind speed and direction, and wave action but, by multiplying the reported densities by 4.4, the number of fish caught h^{-1} can be approximated.

A Wilcoxon signed rank test on pairs of variables was performed, comparing the densities of the individual 5-m and 10-m depth hauls for each locality, to test for depth preference of bib and whiting.

7.2.3 Stomach analysis

For each month 15 to 20 individuals of each species were selected at random for stomach analysis. Because of the low number of stomachs examined for November and December data were pooled for these months. In total 97 bib and 101 whiting stomachs were analyzed. All items in the stomach were identified, if possible to species level, and measured. The original ADW of the prey, prior to ingestion was calculated from length-ADW regressions obtained for prey from the same area (K. Hostens, unpublished data and Chapter 8, Appendix 1). Prey importance is expressed both numerically and gravimetrically.

Dry weight of the stomach content (110°C for 2 to 4 h) was measured for the calculation of the fullness index (FI) (Berg 1979). For statistical purposes, FI was arcsin-transformed (Sokal & Rohlf 1981). About 80 % of the fish found in the stomachs could be identified, at least to genus level, by comparing skeletal elements to a reference collection. Unidentified fish were apportioned in accordance to the numerical or gravimetric percentages of the identified ones (Hislop *et al.* 1991).

The diversity of the diets of both species, a measure of niche breadth, was calculated as Shannon-Wiener H' (Washington 1984):

$$H' = - \Sigma_i p_i \log p_i$$

where p_i is the proportion of the number prey of the ith species in the diet over the total number of items in the diet.

7.2.4 Growth, mortality, production, and consumption

Growth is measured as the increase of mean length of O- group fish per month. The instantaneous mortality rate Z is defined as the decrease in density of O-group fish in the study area and is calculated from the linear regression equation fitted through the ln transformed densities (bib: June through December; whiting: June through October).

Total production P of the cohort over the time period considered is:

$$P = \Sigma \tau P$$

where the monthly production τP can be estimated as:

$$\tau P = \tau \hat{w} \times (N_t + N_{t+\tau t})/2$$

where N_t is the density at time t and $\tau \hat{w}$ is the mean growth increment for this month (Crisp 1984).

Food consumption was estimated directly from the stomach content data using Jones' (1974) model. This model estimates the stomach evacuation rate r (in g h^{-1}) from:

$$r = S^{0.46} \times (L/40)^{1.4} \times Q \times 10^{0.035(T0-Tc)}$$

with S the average weight of the stomach content (g wet weight), L the total length of fish in cm, Q the rate of evacuation for a 1 g meal of a stated food type of a 40 cm fish at temperature T_c and T_0 the temperature of the sea water when sampling. Patterson (1985) gives an erroneous formulation of the same model with 40/L instead of L/40. It seems probable that Patterson's calculations have been done with the correct formula, though this cannot be verified from the paper. For use in the model, ADW measurements were multiplied by five in order to convert to wet weight. After the calculations they were converted back to ADW.

Judging from stomach fullness data in Robin & Marchand (1986) bib feed at about the same rate throughout a 24 h cycle. Similarly, Gordon (1977b) finds little variation in whiting stomach fullness over 24 h. Patterson (1985) reports an early morning peak and an evening dip in stomach fullness of whiting. Around noon stomach fullness is average. Robb (1981) finds a two-peaked feeding periodicity in whiting. One of the peaks is around midnight, the other around midday. As both peaks are of the same magnitude stomach content weights of fish collected during daylight hours can be assumed to be representative for the entire 24 h. For the fish part of the stomach content, a Q-value of 0.26 was used and for the crustacean part a Q-value of 0.19 (Jones 1974). The latter value was also used for the rarely consumed non-crustacean invertebrates. Assuming equi-

librium between intake and consumption, the daily food intake C could be calculated:

$$C = r \times 24$$

where r is the stomach evacuation rate as estimated from Jones' model. Daily food intake C is then expressed as φ, the daily feeding coefficient or the percentage of its body weight the average O-group fish consumed on that sampling date. For bib φ was also calculated according to Pennington (1985), *i.e.* applying Jones' model to the individual fish and averaging afterwards.

Total (or annual) consumption A over the time period considered is then estimated as:

$$A = \Sigma_d \varphi_m \hat{W}_d$$

with φ_m the daily feeding coefficient for the month (or intersampling interval) considered and $\hat{W}_d$ the average population biomass linearly interpolated between two sampling dates (d = 164 and 335).

A P:C ratio or "ecological efficiency" or "conversion efficiency" is calculated from production (P) and consumption (A) values. Gross conversion efficiency is the ratio of the growth increment and the reproductive output over food intake. As O-group gadoids are juvenile, reproductive output can be assumed to be zero and the P:C ratio is equivalent to the net conversion efficiency.

With the partitioning of the food (in weight terms) over the various prey types for each month, the annual consumption of the different prey types is estimated.

Food consumption was also calculated using a P:C ratio of 0.34, as established for I-group cod by Pihl (1982). According to the data in Jones & Hislop (1978) net conversion efficiencies do not seem to differ substantially between different gadoid species. For whiting Jones & Hislop (1978) report an average P:C of 0.3 but there is a tendency for it to be higher in smaller fish. The 0.34 of Pihl (1982) therefore seems acceptable.

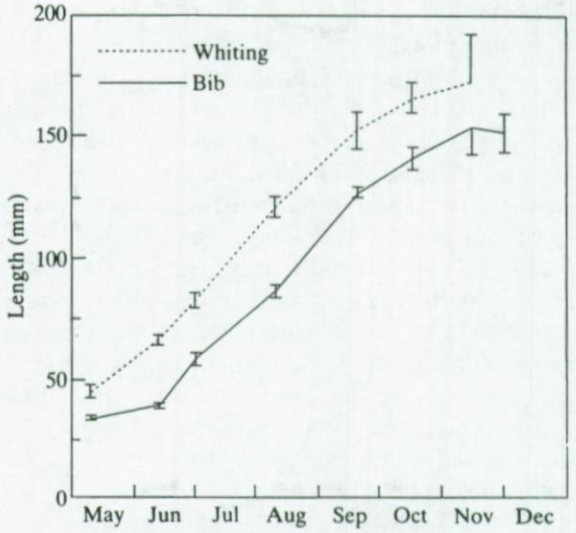

Fig. 7.6 Growth of O-group bib and whiting: mean standard length per month with standard errors

7.3 Results

7.3.1 Growth, density, and spatial distribution

The observed relationship between total length (TL) and standard length (SL) was:
TL = 1.157 + 1.084 SL (n = 111, r^2 = 0.999) for whiting and
TL = 2.35 + 1.102 SL (n = 78, r^2 = 0.97) for bib.

The observed length-weight relationship was:
ADW=7.25 10^{-7} $SL^{3.293}$ (n=45, F=7490, p<0.001) for bib, and
ADW= 1.59 10^{-6} $SL^{3.066}$ (n=47, F=6124, p<0.001) for whiting.

The first O-group bib (n = 5) and whiting (n = 52) were caught in the study area in May, though smaller postlarvae had already been caught with the finer-meshed nets of the hyperbenthic sampler (Hamerlynck & Mees 1991) in April (J. Mees, un-

Table 7.4 Month and day number of sample counting from 1 January (d_s), density (N 10^{-3} m^{-2}), and biomass (gADW 10^{-3} m^{-2}) with standard errors for O-group bib and whiting

		Trisopterus luscus		*Merlangius merlangus*	
Month	d_s	Density	Biomass	Density	Biomass
May	130	0.4±0.3	0.04±0.03	4.6±2.3	0.9±0.4
Jun	164	72.6±52.3	13.3±9.6	28.1±14.7	21.2±11.9
Jul	182	18.1±7.3	11.3±3.8	11.0±4.1	15.2±5.7
Aug	222	11.3±5.8	23.5±14.8	5.8±2.8	23.5±12.4
Sep	263	12.7±4.6	85.8±32.1	3.5±1.1	29.6±10.6
Oct	290	7.0±2.3	68.0±22.5	3.7±1.9	40.0±19.4
Nov	319	1.3±0.5	16.7±7.0	0.2±0.2	2.7±1.9
Dec	335	1.1±0.6	12.6±6.4	0.2±0.1	1.9±1.3

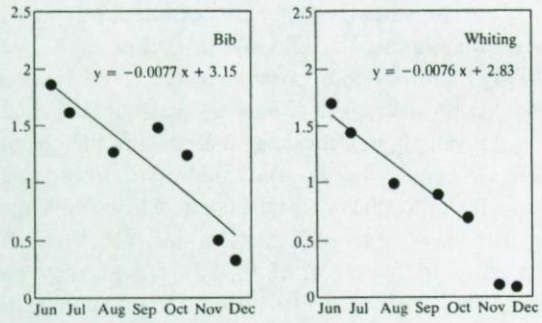

Fig. 7.7 Density of O-group bib and whiting (ln transformed): means per month with the regression lines for mortality

published data). Growth was quite fast with mean lengths of the cohorts increasing from less than 50 mm in May to 154 mm for bib and 173 mm for whiting in November (Fig. 7.6). In December there was a slight decrease in mean length for bib. No mean length was calculated for the two O-group whiting caught in December.

From June onwards bib densities were about double those of whiting (Table 7.4). By November O-group fish of both species had mostly left the area or had died.

Both species had a strong preference for the 10 m below MTL depth stratum. The Wilcoxon test was highly significant ($p<0.001$) for both species (bib: Z= -4.8; whiting: Z = -3.6). There was a clear maximum of abundance in the inner part of the ebb-tidal delta of the Grevelingen (Fig. 7.5b, c). For whiting this remained so throughout the year, for bib the centre of gravity of the distribution shifted towards the ebb-tidal delta of the Oosterschelde from August onwards (Fig. 7.5d).

7.3.2 Mortality

The linear regressions fitted through the (ln transformed) densities *versus* time are highly significant (r^2_{bib} = 0.94, $r^2_{whiting}$ = 0.81, $p<0.01$ in both cases) (Fig. 7.7). From these regressions the instantaneous total mortality rate was estimated at 0.0077 day^{-1} (0.77 % day^{-1}) for bib and 0.0076 day^{-1} (0.76 % day^{-1}) for whiting. This corresponds to approximately 21 % $month^{-1}$ in both species.

7.3.3 Production

Total production per unit area of subtidal seabed for the O-group (June through December 1988) amounted to 0.13 gADW m^{-2} $year^{-1}$ for bib and to 0.06 gADW m^{-2} $year^{-1}$ for whiting. The P:B ratio for the time period considered was 4.5 for bib and 3.8 for whiting.

7.3.4 Feeding and food consumption

Average fullness index (FI) (backtransformed) over the study period was 1.75 (S.E. 0.004) for bib and 1.39 (S.E. 0.004) for whiting. Empty stomachs were rare, only three being found in bib and only one in whiting. There was no clear seasonal pattern in the FI (Table 7.5).

Numerical and gravimetric percentages of the main food categories are shown in Fig. 7.8. After feeding exlusively on calanoid copepods both species shifted to fish, mysids, and amphipods at about 50 mm SL. From about 100 mm SL both species fed nearly exclusively on shrimp and small fish.

According to Jones' model, bib consumed 0.29 gADW m^{-2} $year^{-1}$, whiting 0.18 gADW m^{-2} $year^{-1}$. Daily feeding coefficient φ was between 4 and 6 % of body weight in summer and declined to 2 to 3 % in autumn. For bib there is little difference between φ as estimated through Pennington's procedure and the more classical approach using the average stomach content (Table 7.5).

The P:C ratio was 0.45 for bib and 0.36 for whiting. Using the P:C ratio of 0.34 (Pihl 1982) total consumption amounted to 0.38 gADW m^{-2} $year^{-1}$ for bib and to 0.19 gADW m^{-2} $year^{-1}$ for whiting. A major part of this consumption consisted of a restricted number of species (Fig. 7.9), mainly the brown shrimp *Crangon Crangon*, two species of goby (*Pomatoschistus minutus* and *P. lozanoi*) and larval and early postlarval herring (*Clupea harengus*) and sprat (*Sprattus Sprattus*). In bib, which has a more diverse diet (Shannon-Wiener H'= 1.05) than whiting (H'=0.61), other fishes such as young sandeel *Am-*

Table 7.5 Number of fish caught (N_c), number of stomachs analysed (N_s), mean fullness index with standard error (F.I. ± S.E.), total number of prey items (N_p), daily feeding coefficient according to Jones (φ_j), according to Pennington (φ_p) for O-group bib and whiting

	Trisopterus luscus						*Merlangius merlangus*				
	N_c	N_s	F.I. ± S.E.	N_p	φ_j	φ_p	N_c	N_s	F.I. ± S.E.	N_p	φ_j
May	5	4	0.9±0.09	184	–	–	57	17	1.6±0.02	1388	–
Jun	902	21	1.8±0.01	856	4.7	5.1	349	19	1.1±0.03	328	4.2
Jul	234	14	3.3±0.01	247	5.9	6.4	143	17	1.4±0.03	241	4.4
Aug	147	12	1.9±0.05	149	5.8	5.5	75	15	1.4±0.05	137	6.0
Sep	165	16	1.0±0.02	237	3.2	3.3	45	14	1.7±0.02	55	4.8
Oct	90	20	1.8±0.02	344	3.1	3.1	48	15	1.4±0.03	67	2.8
Nov-Dec	31	10	1.4±0.05	93	2.5	2.1	5	4	0.8±0.03	12	1.8

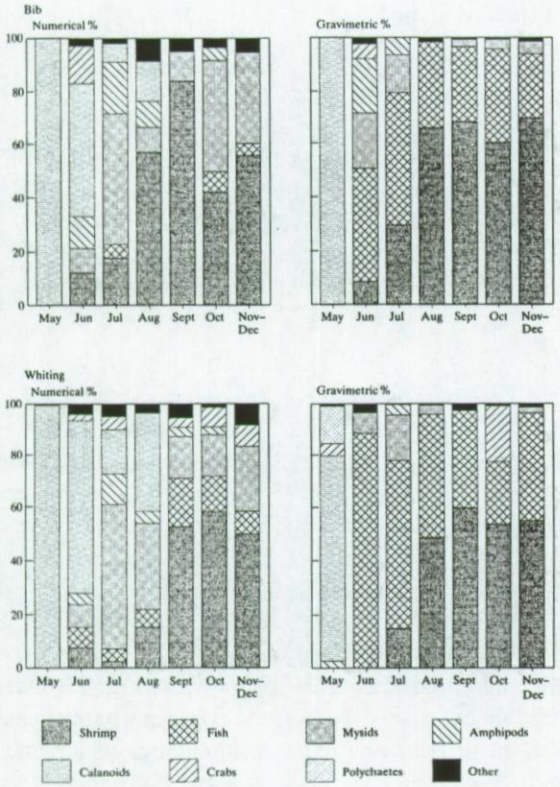

Fig. 7.8 Numerical and gravimetrical food composition for bib and whiting

modytes tobianus, dragonet *Callionymus lyra*, early postlarval flatfish, and gadoids occurred on a par with juvenile clupeids. The only other important prey were three mysids *Gastrosaccus spinifer*, *Schistomysis kervillei*, and *S. spiritus* and two amphipods *Gammarus crinicornis* and *Atylus swammerdami*.

7.4 Discussion

The estimates of all the variables in this paper are subject to various sources of bias. Most of these have been discussed by Patterson (1985) but in the present study the estimate of net efficiency, defined as the percentage of O-group gadoids, feeding on or above the sampled surface area, caught in the net, is an added major source of uncertainty.

The assumption that net efficiency is only 20 % is something of a wild guess. Following Kuipers (1975) there are four possible ways for fish in the trawl path to escape from an approaching beam trawl: through the meshes, underneath the ground rope, over the beam, and sideways. Escapement through the meshes can be assumed to be low once the fish have reached a certain size, i.e. from July onwards. Creutzberg *et al.* (1987), though they state that pelagic fish such as whiting are not supposed to be influenced by the number of tickler chains on a beam trawl, found that the slope relating numbers caught on sandy bottoms to the number of tickler chains used was actually significantly different from zero in whiting. Variability in whiting catches was high but using three tickler chains Creutzberg *et al.* (1987) caught 1.5 times more whiting than with one tickler chain. Catches reached a plateau at three tickler chains. Therefore there seems to be some escapement under the gear when using only one tickler chain on sandy bottoms. Engås & Godø (1989) also report on substantial numbers of small gadoids escaping under an, admittedly quite different, trawled gear. The observations of Creutzberg *et al.* (1987) put maximum efficiency at 68 %. Bib and whiting are fast swimmers, so an unknown proportion, especially of the larger fish, can be expected to be able to avoid the gear by moving up or sideways. Moreover, as bib and whiting are pelagic at first and, even when becoming demersal, do not spend all of their time in close proximity to the bottom, some proportion of the population is also out of reach of the gear, the headrope of which is at 0.55 m from the bottom. Net efficiency is therefore unlikely to be over 50 % and in this study it was assumed to be a lot less. This means there are considerable margins of uncertainty to the estimates based on this assumption. If efficiency were 40 % density, biomass and production would only be half of the estimates given. More detailed studies on net efficiency, along the lines proposed by Kuipers *et al.* (1992), are clearly warranted. Only then can studies of fish trophodynamics be expected to match the accuracy of macrobenthic studies.

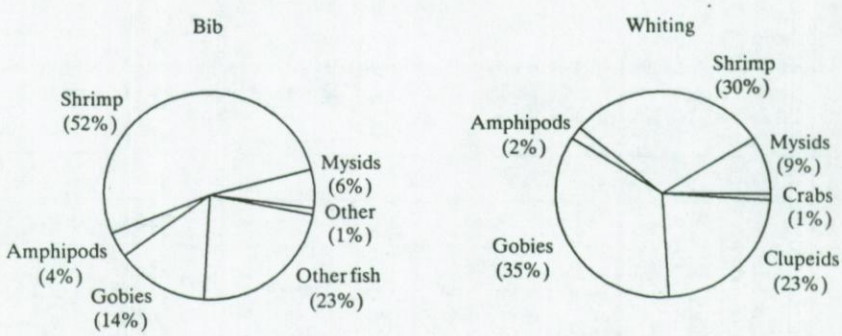

Fig. 7.9 Partitioning of food consumption by O-group bib and whiting (June through December) for the main prey categories

Growth as recorded in this study closely matches the results from other studies: in Moroccan waters (Coupé & Maurin 1955) and on the Atlantic coast of Spain (Oliver 1949) O-group bib averaged between 125 and 130 mm SL by the end of the first growth season. By February of the next year the model class reaches 150 mm SL in the southern North Sea (Desmarchelier 1985a). Fish collected from the intake screens of power stations have a seemingly slower growth: model length class of bib in the Severn estuary increased from 40-49 mm SL in August to 70-79 mm in November-December (Claridge & Potter 1984). Similarly, O-group whiting in the Severn estuary grew from 60-70 mm SL in June-July to only 100 mm SL in December (Henderson & Holmes 1989). This slow "growth" is probably an artefact of the collection method. Perhaps the larger O-group gadoids have sufficiently high swimming speeds to avoid being sucked into the power station. On the Scottish west coast whiting grew from about 100mm SL in July to about 160 mm SL in November (recalculated from Gordon 1977a). This is very similar to growth in Kiel Bight (Arntz & Weber 1972) and closely resembles the results of the present study.

As in other studies fish "growth" as defined here is a combination of true growth of individuals, predation (possibly size-selective), migration (probably also dependent on size), and mesh selection in an unknown mixture. Mean lengths in November and December are less reliable because of the low numbers of O-group caught. The apparent length decrease of bib in December may be caused by differential migration, the largest fish leaving the area first. The same phenomenon was observed in other gadoids (Cooper 1980).

As can be judged from the standard errors of the densities (Table 7.4) the spatial distribution of both species is very patchy. The concentration in the ebb-tidal delta of the Grevelingen, which is especially strong in the early part of the year and is most pronounced in bib, may be partly caused by passive transport into the area. The current patterns in the ebb-tidal delta of the Grevelingen create a sink for mud and detritus. Other neutrally buoyant particles *e.g* macrobenthos larvae, larval decapods, and fish eggs and larvae may also be trapped in the area (Chapter 4-Add.). According to Cooper (1980) O-group gadoids in Scottish waters reach their nurseries mostly through active migration. Just like postlarval flatfish (Rijnsdorp *et al.* 1985), juvenile gadoids are probably rather versatile. They can make use of the residual current for passive drift but, through vertical migration, they may also be able to make use of the tidal currents to move in the opposite direction.

The observed shift in bib distribution from the ebb-tidal delta of the Grevelingen to the ebb-tidal delta of the Oosterschelde may be partly due to migration, but there may be an add-on effect of O-group bib leaving the Oosterschelde proper. This second effect may also form the basis of the slight increase in density of bib in September and of whiting in October (Table 7.4).

The estimates of the instantaneous mortality rate are a combination of natural mortality, (indirect) fishing mortality and migration. Indirect fishing mortality of O-group gadoids in the area is thought to be low since few shrimp trawlers operate in this part of the Voordelta. Migration can be an important contributing factor as it is well known that O-group bib and whiting migrate to deeper areas by the end of their first growth season. Migration is thought to be the main cause for the sudden decrease in whiting densities after October. Therefore, the last 2 months were not used for the calculation of Z in this species.

The production:biomass (P:B) ratio calculated is higher than the often used P:B = 2.75 (Elliott & Taylor 1989) or 2.5 (Chapter 3). These last two figures may be valid for mixed age groups of fishes but less so for the O-group.

For whiting there is close similarity between consumption estimated directly from the stomach contents and indirectly from production using a production: consumption (P:C) ratio of 0.34. For bib the estimate using Jones' model is about 25 % lower than using the P:C ratio. Possibly Jones' model has limited applicability for the deeper bodied and shorter lived *Trisopterus* species. The feeding coefficient φ is in close agreement to the findings of Daan (1973) who gives 5.3 % for North Sea cod of 100 mm (probably total length, measurement procedure not mentioned in Daan (1973)) and 2.5 % for cod of 200 mm.

Food preference at different sizes closely resembles the pattern observed by other authors (see references in the introduction): first calanoids, then mysids and amphipods and finally shrimp and small fishes.

Our estimate of the P:C ratio, or ecological efficiency, seems high for bib, but for whiting it is closely similar to the estimate of Pihl (1982) for I-group cod and to the estimate of Jones & Hislop (1978) for different gadoid species. All these estimates are much higher than the 0.11 to 0.18 suggested for whiting by Patterson (1985), though his data did not include O-group fish. Moreover, if consumption was calculated by Patterson (1985) using the stated formula, it may have been seriously overestimated, leading to a very low P:C.

Though Pennington (1985) showed that one should first raise the individual weights in the stomachs to a certain power (0.43 in the case of Jones' model) and then calculate the mean to find an unbiased estimator of food consumption, this procedure was not followed in the present study, nor by Hislop *et al.* (1991). The possible consequences of this are illustrated in a very extreme example given in Ursin *et al.* (1985) where consumption was overestimated

by over 40 % using our procedure. However, as long as variability in the amount of food in the stomachs of the fish is low, which, in the present study, is the case for both species, the final result of both procedures is rather similar and the calculations are very substantially simplified using the average of stomach content per sample as the input to Jones' model. Thus, in bib, there was on average less than 0.4 % difference between percent body weight consumption using Pennington's procedure and the simpler approach. From the variability in stomach contents in whiting it seems highly likely that, if any, the difference between the two procedures for whiting would have been of the same order of magnitude. However, Pennington's procedure should be used in species taking single meals of large and heavy items with long (*e.g* several days) non-feeding intervals between two meals.

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CHAPTER 8 THE DIET OF BROWN SHRIMP *CRANGON CRANGON* (L.) IN THE WESTERSCHELDE ESTUARY

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Abstract. *Brown shrimp Crangon crangon was sampled during several surveys in the Westerschelde estuary. Diurnal samples were taken in the brackish subtidal, seasonal samples in the marine and brackish subtidal, and monthly samples in the brackish intertidal part. The diet of C. crangon was studied through stomach content analyses, which were sometimes complicated due to the presence of sand grains and unidentifiable remains. On average 36 % of the stomachs examined were empty, 33 % had few (highly digested) remains (mainly from crustaceans), and 31 % contained many (partly digested) prey items. Still, clear differences in density and feeding of C. crangon were recorded at several scales. Density, feeding intensity and prey diversity showed mixed tidal-diurnal patterns, with a dominance of the tidal pattern, and more feeding and a higher trophic diversity at high water. On a seasonal scale, density and prey diversity were highest during summer, both sub- and intertidally. Stomach fullness was higher in (early) spring, although this was partly influenced by the moment of sampling compared to the tidal phase. C. crangon had a higher prey diversity in the intertidal (21 out of 32 prey categories), but with an overall dominance of small crustaceans, i.e. mysids, amphipods and copepods. During the 24-h surveys, mysids (mainly Neomysis integer and Mesopodopsis slabberi) were the most important prey items, day and night (>60 % in percentage occurrence (%F), abundance (%N) and weight (%G)). Seasonally, mysids were important prey items in spring and summer, both in the marine (>55 %F-N-G, mainly Gastrosaccus spinifer) and brackish (>40 %F-N-G, N. integer and M. slabberi) subtidal. In the latter, mysids were replaced by amphipods (20 %F-G, 60 %N, Corophium and Bathyporeia) in autumn and winter, which paralleled the seasonal patterns in prey abundance and prey availability. Feeding behaviour was dependent of habitat type, rather than body size. Larger shrimps did not necessarily feed on larger mysids or amphipods. In the brackish intertidal, mysids were infrequently preyed upon. In this subhabitat, shrimps were on average 10 mm smaller than in the subtidal, and in terms of abundance, copepods (30 %F-N) were gradually replaced in the diet by amphipods (>25 %F-N-G) with increasing size of C. crangon. Other less important prey items for the different surveys were ostracods, cyprid larvae, shrimps, bivalves (mainly Mytilus spat), polychaetes (mainly Nereidae), gastropods (mainly Littorina), and fish. Daily consumption amounted to 0.01-0.12 g ashfree dryweight (ADW) per day. It is suggested that C. crangon mainly foraged in the hyperbenthal waterlayer (mostly during night), supplemented with some food from the epibenthal layer during the day. The presence of many mysid statoliths in the stomachs, additionally proved the importance of mysids in the shrimp diet, but possibly led to overestimated consumption values. Minimum and maximum values (either based on measured prey weights in the stomachs or on recalculated prey weights prior to ingestion) were on average 1 to 5 % bodyweight per day in the subtidal, and 4 to 14 %BW d^{-1} intertidally. Yearly consumption was 1 to 8 gADW m^{-2} yr^{-1}, both sub- and intertidally. Shrimp predation could have a large impact on the mysid population, as on average 10 to 35 % of the mysid standing stock was consumed per day.*

8.1 Introduction

Estuaries are widely recognized as important nurseries and feeding areas for fish and macro-crustaceans, characterized by high numbers of only a few species, and macro-crustaceans outnumbering the fish species (overview in Elliott & Hemingway 2002). The brown shrimp *Crangon crangon* (L) is the commonest shrimp species in shallow coastal and estuarine waters of the northeastern Atlantic (Holthuis 1980). For example, in the Westerschelde estuary, brown shrimp numerically constituted >80 % of the total epibenthic community, and the total average numbers in the subtidal was estimated at 3 10^8 individuals at the end of the 1990s (Chapter 2, Chapter 5). *Crangon crangon* is commercially fished on the North Sea coasts, with an average annual landing of 2.6 10^4 tonnes (consumption shrimps) between 1995 and 2000, >80 % supplied by Germany and the Netherlands (Anonymous 2001).

Several aspects of its biology and ecology are well studied. *Crangon crangon* is a benthic (bottom-dwelling) species with a preference for sandy sediments, where they quickly can bury themselves to escape from predators (Pinn & Ansell 1993). It is known to be more active during the night (*e.g.* Burrows *et al.* 1994). The life history and population dynamics have been studied in several areas (*e.g.* Tiews 1970, Kuipers & Dapper 1981, del Norte-Campos & Temming 1998, Oh *et al.* 1999). For the Westerschelde estuary, Cattrijsse *et al.* (1997) showed that postlarvae of *C. crangon* grow up in the brackish saltmarsh creeks, with a continuous release of small juveniles (>15 mm) from early spring till late autumn into the estuary proper. It is a euryhaline and resident species both in the main subtidal channel and on the intertidal sandflats, and highly abundant in the brackish reaches of the Westerschelde (Hostens *et al.* 1996, Chapter 5). Also in the more upstream parts of the Schelde estuary brown shrimp was common, but with a limited distribution due to oxygen deficiency during most part of the year (Maes *et al.* 1998a).

Crangon crangon is an important key species in many food-chains in European waters (Hemingway & Elliott 2002). It serves as an important prey for both juvenile and adults of several fish species (*e.g.* Costa & Elliott 1991, Moreira *et al.* 1992, Henderson *et al.* 1992, Berghahn 1996, Chapter 7-Add.). Also, the feeding ecology of *C. crangon* is well studied. It has a structuring influence on bivalve populations (mainly *Macoma balthica*) in several systems, by cropping the siphons (Kamermans & Huitema 1994) or by feeding on bivalve spat (van der Veer *et al.* 1998). It maintains a population regulating function as predator of the smallest length classes (<30 mm) of plaice *Pleuronectes platessa* (*e.g.* Gibson *et al.* 1995, Wennhage & Gibson 1998). They are considered opportunistic carnivores, with prey selection dependent on prey availability and sediment type (Pihl 1985, Oh *et al.* 2001).

Preliminary stomach analyses showed that mysids were a major prey for *C. crangon* in the Westerschelde. The importance of mysids in the diet of brown shrimp was confirmed by only one recent study (Oh *et al.* 2001). In most other studies brown shrimp was found to predate mainly on benthic (meio- and macro) infaunal species (*e.g.* Evans 1984, Pihl & Rosenberg 1984, Henderson *et al.* 1992). As feeding characteristics can vary considerably from one habitat to another, this study focuses on the (underestimated) importance of hyperbenthic prey - and mysids in particular - in the diet of juvenile (and adult) brown shrimp *C. crangon* in several subhabitats from the Westerschelde estuary.

8.2 Materials and methods

8.2.1 Sampling

The estuarine population of brown shrimp *Crangon crangon* was sampled during several surveys in the Westerschelde estuary (Fig. 8.1), situated in the southwest Netherlands (51°24'N; 4°05'E). The Westerschelde could be divided (near Hansweert) into a marine and a brackish part from Vlissingen in the mouth to the Dutch/Belgian border, based on the epibenthic assemblages (Chapter 2). The subtidal surface areas of the marine and brackish parts are 130 and 40 km², respectively (Vroon *et al.* 1997). The Westerschelde is characterized by a marked salinity gradient (on average 26 ± 3 psu in the marine part, and 17 ± 5 psu in the brackish part) (Chapter 5, and this chapter). The total intertidal surface area is 83 km², in the brackish part divided as 14 km² tidal sandflat and 20 km² tidal mudflat (Vroon *et al.* 1997). The subtidal is characterized by sandy sediments: median grain size 330 ± 97 µm in the marine part and 240 ± 55 µm in the brackish part (Chapter 5). The high intertidal part of the brackish sandflat of Valkenisse had a mixed sand-silt sediment, with a median grain size 168 ± 40 µm and an average concentration of 10 % silt. Hyperbenthic organisms (mainly mysids and amphipods) are present in high numbers in the subtidal (Mees *et al.* 1993b); macrobenthic organisms (mainly bivalves, polychaetes and amphipods) are abundant in the intertidal and almost absent subtidally (Ysebaert *et al.* 1998). More details on the environmental and ecological properties of the Westerschelde are given in Meire & Vincx (1993), Heip & Herman (1995) and Van Damme *et al.* (1999).

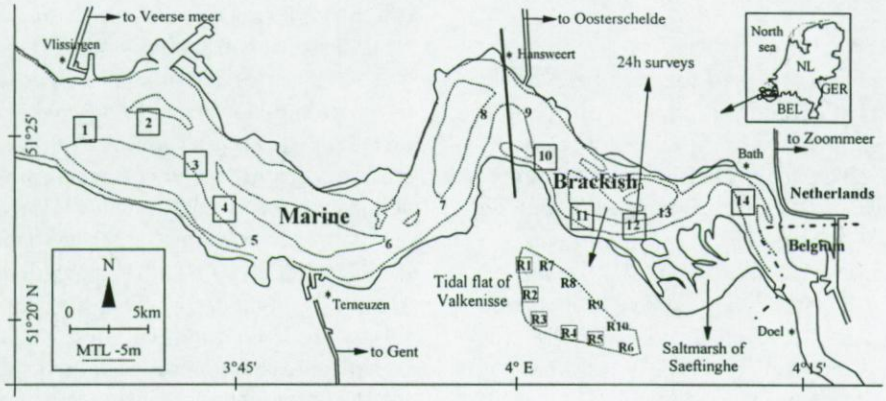

Fig. 8.1 Map of the Westerschelde estuary, showing the sampling locations for the different surveys: 24-h surveys (subtidal, station 12); seasonal surveys (subtidal, 14 stations) and monthly surveys (intertidal, 10 stations). Numbers in squares indicate the samples from which stomachs were selected from analysis

For the stomach content analyses, shrimps were collected from selected samples from the following campaigns (Table 8.1, Fig. 8.1): (1) two 24-hour surveys between 18 and 19 September 1991 (2-hourly, 13 samples) in a brackish subtidal station (station 12), sampled with a 3-m beam trawl (6x6 mm cod-end) and a hyperbenthic sledge (1 mm² mesh); (2) four seasonal surveys between August 1999 and May 2000 at 14 stations in the marine and brackish parts of the subtidal channel (on average MTL –12 ± 2 m), sampled with the same 3-m beam trawl; (3) 6 monthly surveys between April and October 1992 at 10 stations on the brackish intertidal sandflat of Valkenisse at 1 m below mean tidal level (MTL), sampled with a 2-m beam trawl (5x5 mm cod-end). For the 24-h trawl survey, the 2 o'clock sample was badly preserved. For the 24-h sledge survey, no shrimps were available for stomach content analyses from the 14, 18 and 8 o'clock samples. The seasonal and intertidal surveys were conducted during daytime. The tidal phase at which samples for stomach contents analyses were taken, is given in Table 8.1. The intertidal was sampled during a period of 2 hours before and 2 hours after high water. More details on these sampling surveys are given in Muhando (1992) for the 24-h trawl and 24-h sledge surveys, in Chapter 5 for the subtidal marine and brackish surveys, and in Hostens *et al.* (1996) for the intertidal survey.

Table 8.1 Overview per survey (daytime samples, except 24-h surveys) of the tidal phase, the number of stomachs analysed per sex; modal, minimum and maximum total length of *C. crangon* analysed; percentage stomachs with sand grains (S_S); stomach fullness as percentage with many remains (S_M), few remains (S_F) and empty (S_E); and percentage bodyweight consumed per day (%BW d^{-1}) based on the recalculated weight of prey items prior to ingestion, and taking into account an 8-h feeding period for the seasonal and intertidal surveys

survey/ period	salinity zone	tide	# stomachs		total length (mm)		sand	stomach fullness			%BW d^{-1}
			female	male	mode	min-max	%S_S	%S_M	%S_F	%S_E	
24-h surveys (subtidal)											
18-19 Sep 1991 (24-h trawl)	brackish	cycle	67	116	36	25-54	51	19	38	43	4.9
idem (24-h sledge)	(station 12)	cyce	58	121	35	20-53	24	36	13	51	7.9
Seasonal (subtidal)											
2 Sep 1999 (summer)	marine	ebb	17	13	47	26-54	37	20	37	43	4.4
	brackish	ebb	33	14	45	21-49	74	19	70	11	9.6
25 Nov 1999 (autumn)	marine	low	2	13	39	22-51	33	-	40	60	1.5
(	brackish	flood	30	18	33	22-59	63	27	44	29	4.5
16 Feb 2000 (winter)	marine	high	7	8	33	24-50	33	7	53	40	2.5
	brackish	flood	46	2	41	19-51	27	44	23	33	6.1
17 May 2000 (spring)	marine	flood	9	7	35	30-61	88	56	44	-	8.3
	brackish	flood	43	2	30	24-50	47	33	38	29	4.3
Monthly (intertidal)											
2 Apr 1992	brackish	high	10	5	30	16-46	40	55	9	36	6.3
11 May 1992	(Valkenisse)	high	11	4	40	14-47	87	42	42	16	9.8
9 Jul 1992		high	11	4	34	23-36	40	67	13	20	16.1
6 Aug 1992		high	12	3	28	22-38	93	67	33	-	16.6
7 Sep 1992		high	8	9	25	19-45	82	50	44	6	10.0
7 Oct 1992		high	9	7	28	18-41	94	67	33	-	14.4
											12.9
Total			**373**	**346**			**47**	**31**	**33**	**36**	

8.2.2 Analyses

All shrimps were wet weighed together per sample. A subsample was stored in 4% formalin, after killing the animals in warm freshwater to prevent regurgitation of the stomach contents. Density, total length (L_t, mm) and wet weight (g) were recorded. From the wetweight ratio subsample/total sample and the number of shrimp in the subsample, the density per m² was calculated. The total biomass per sample (gADW m^{-2}) could be recalculated from the wetweight ratio and the length – ADW (ashfree dry weight) regression given in Appendix 1. The density and growth patterns are briefly touched upon, the biomass values are used in the consumption calculations. More details on the seasonal patterns are given in Chapter 5.

Only for the stomach analyses shrimps were sexed, based on secondary sex-characteristics (endopod of first pleopod broader and leaflike in females, and presence of the *appendix masculina* on the second pleopod in males). Stomach analyses were carried out on 719 individuals, ranging in total length from 14 to 61 mm, selected proportionally to the length-frequency distributions for the different surveys (Table 8.1). The number of empty stomachs and the number of sand-grains in the stomachs were recorded.

Prey items were identified as detailed as possible. Unidentifiable remains (if possible further divided as originating from mysids, amphipods, crustaceans, polychaetes or bivalves) were regarded as 1 prey item and weighed as such (mg ADW). Other parts of the different prey items were measured and recalculated to a length prior to ingestion (Berg 1979). From these prey lengths the weight of the prey at ingestion (mg ADW) could be calculated, to establish the gravimetrical diet composition. All conversion regressions and assigned values are given in Appendix 1. In many stomachs only the statoliths (located in the endo-uropods) of mysids were present, sometimes in high numbers (up to 49). As these hard parts remain in the stomach for a longer time, the estimation of the possible number of mysids consumed per feeding time was based on the following rule: 1 to 6 statoliths in a stomach = 1 mysid taken; 7-12 = 2; 13-18 = 3; 19-24 = 4; 25-32 = 5; 33-40 = 6; 41-49 = 7.

Stomach 'fullness' was described in 3 categories: empty (S_E), few remains (S_F) and many remains (S_M), with the distinction between the latter two categories based on whether only unidentifiable remains (including statoliths of mysids) were present in the stomach or if clear (partly ingested) prey items were present. Log-linear analysis, based on two-way contingency tables or crosstabulated frequency data (Sokal & Rohlf 1997), was used to test the association between stomach fullness and factors related to life history (sex) and feeding activity (day-night, tidal, seasonal and spatial models).

A series of common indices were used to determine diurnal, seasonal and spatial patterns in the diet composition of *C. crangon*: fullness index (FI) of the stomachs, frequency of occurrence (%F), relative abundance (%N) and weight (%G) of the different prey items, lumped into larger 'taxonomic' categories (see Hyslop 1980), and trophic diversity as Hill's number N_1 (Hill 1973). This was done per sampling survey, per 2-hour interval for both 24-h surveys, per season and subarea for the subtidal survey, per month for the intertidal survey, and per 2mm length-class for the different surveys. All indices were based on the non-empty individual stomachs, except the fullness index which was calculated as the ratio between average weight of stomach content (excluding sand-grains) and weight of a shrimp of modal length per sampling moment (i.e. time of the day, season or month). The relationship between predator and prey size of 3 mysid and 2 amphipod species was investigated through linear regression.

The diurnal and seasonal predation impact of *C. crangon* on the mysid populations (expressed as number of mysids removed per m² per day) was based on the average mysid density (from the hyperbenthic sledge samples) and the number of mysids consumed by all shrimp (stomach content analyses and shrimp densities based on the beam trawl samples) for a certain sampling moment. As most mysids were either partly or completely digested, it was assumed that the mysids were 50 % consumed at the moment of sampling and 50 % 2 hours earlier for the 24-h trawl survey, in order to make a direct comparison between the number of mysids present and consumed. For the seasonal consumption estimates it is assumed that what is present in the stomach is representative for a 24-h feeding period. Mysid data were taken from Muhando (1992) for the 24-h survey, and from Chavatte (2001) for the subtidal survey.

Percentage of bodyweight consumed per day (%BW) was calculated in 2 ways for the different surveys: based on 'experimentally determined' daily rations (DR) as a function of temperature (T, °C) and individual shrimp weight (W, mg ADW) per size class i, derived from the following formula (van Lissa 1977):

$$DR_i = (5.941 - 1.218T + 0.082T^2 - 0.00164T^3) \times W_i \wedge (0.255 + 0.096T - 0.00746T^2 + 0.00016T^3) \quad (1)$$

$$\%BW = (\sum_i (DR \times \check{D}) / \check{G}) \times 100 \quad (2)$$

with $\check{D}$ average density (m^{-2}, here per size class) and $\check{G}$ average biomass (mg ADW m^{-2}) of the shrimp population at a certain sampling moment.

Secondly, %BW (d^{-1}) was based on daily consumption (C_d, mg ADW m^{-2}) derived from the

stomach content analyses, i.e. the average consumption per shrimp in the field per sampling moment (C_S), calculated as the summed weight (mg ADW) of all prey items in all stomachs (either really measured or recalculated prior to ingestion) divided by the number of analysed stomachs per sampling moment. For the 24-h surveys, daily consumptiom is a summation over all hours sampled of C_S and average density ($\check{D}$, here per sampling moment) and corrected over a 24-h period:

$$C_d = \sum_h(C_S \times \check{D}) \times 24/26 \quad (3)$$

For the other surveys, daily consumption was calculated as the product of C_S and $\check{D}$, averaged over the seasons (subtidal) or months (intertidal), and taking into account a feeding period of 8 hours (based on the fact that shrimp mainly feed around high water, see discussion):

$$C_d = avg(C_S \times \check{D}) \times 8 \quad (4)$$

Percentage bodyweight per day was then calculated as:

$$\%BW = (C_d / \check{G}) \times 100 \quad (5)$$

For the calculation of the yearly consumption (g ADW m^{-2} yr^{-2}), C_d was multiplied by 365, assuming the shrimp population was feeding 8 hours a day throughout the year, both in the sub- and intertidal. Again, minimum and maximum values were based on whether the daily consumption was based on the real stomach weight or on recalculations prior to ingestion. By multiplying with the different surface areas, the maximum yearly consumption by the shrimp population was calculated per subhabitat in the Westerschelde estuary.

8.3 Results

8.3.1 Density and growth patterns of the Crangon crangon population

In the 24-h surveys, density of brown shrimp *Crangon crangon* showed a tidal pattern (Fig. 8.3a). For shrimps taken with the beam trawl (24-h trawl survey), highest densities were recorded around high water (max. 26 ind m^{-2}, during the night), and lowest densities around low water (min. 8 ind m^{-2} at sunrise). The modal length class was 30-40 mm L_t. Only few juvenile shrimps (<0.1 ind m^{-2}) were caught with the hyperbenthic sledge (24-h sledge survey). For this survey the tidal pattern was less clear during daytime. Still, higher densities were recorded around both high water peaks (and during darkness).

Seasonally, the average density in the subtidal Westerschelde was highest in summer 1999 (2.8 ind m^{-2} in September, note that this is 10 times lower than in 1991), equal in spring and autumn (1.3 – 1.1 ind m^{-2}), and lowest in winter (0.6 ind m^{-2} in February) (Fig. 8.2a). The total length of the shrimp population caught with a 3-m beam trawl ranged between 15 and 75 mm. There was a small growth increase from winter to autumn in the subtidal, with a yearly modal length of 40 mm. On a spatial scale, shrimp densities were twice as high in the brackish part (on average 1.4 ind m^{-2}) than in the marine part (except in spring). Shrimps were on average 2 mm larger in the marine subtidal.

In the brackish intertidal, large differences were recorded between spring (<0.1 ind m^{-2}) and the summer-autumn months (on average 4.5 ind m^{-2}) (Fig. 8.4a). Intertidal shrimps were on average 10 mm smaller than in the subtidal, with a modal length of 30 mm.

8.3.2 Stomach fullness

At first sight, most stomachs seemed full (the typical dark blot in external dorsal view), but of the 719 stomachs examined 259 stomachs were empty, 237 contained some animal remains, and 223 contained many remains (Table 8.1). Between 24 % (24-h sledge) and 94 % (intertidal) of all stomachs, and >70 % of the non-empty stomachs contained sand (from a few to several hundreds grains per stomach). On average 2 prey items were recorded per non-empty stomach, with a maximum of 7 prey items per stomach in the 24-h trawl survey and 16 prey items per stomach in the brackish subtidal (Table 8.3).

For the 24-h trawl survey and the subtidal marine survey, the number of empty stomachs (S_E) equalled the number of stomachs with few remains (S_F), and only 20% of the stomachs contained many remains (S_M) (Table 8.1). The ranking for the other surveys was: $S_E > S_M > S_F$ (24-h sledge); $S_F > S_M > S_E$ (subtidal brackish); $S_M > S_F > S_E$ (intertidal).

Table 8.2 Summary of the log-linear analyses (χ^2 and significance for maximum likelihood ratio) of sex (2 levels), time of the day (11 and 9 levels), day/night (2 levels) tide (6 levels), season (4 levels), month (6 levels), subarea (2 levels) and subhabitat (2 levels), for 3 different categories of stomach fullness

Comparison	24-h brackish subtidal		subtidal		intertidal
	trawl	sledge	marine	brackish	Brackish
Fullness x sex	9.60 **	0.83 ns	1.05 ns	18.02 ***	3.83 ns
Fullness x time	50.86 ***	25.16 ns			
Fullness x day/night	4.69 ns	7.24 *			
Fullness x tide	36.42 ***	15.12 ns			
Fullness x season			29.42 ***	24.24 ***	
Fullness x month					18.92 *
Fullness x subarea			4.28 ns		
Fullness x subhabitat				19.04 ***	

*** p <0.001; ** p <0.01; * p <0.05; ns not significant

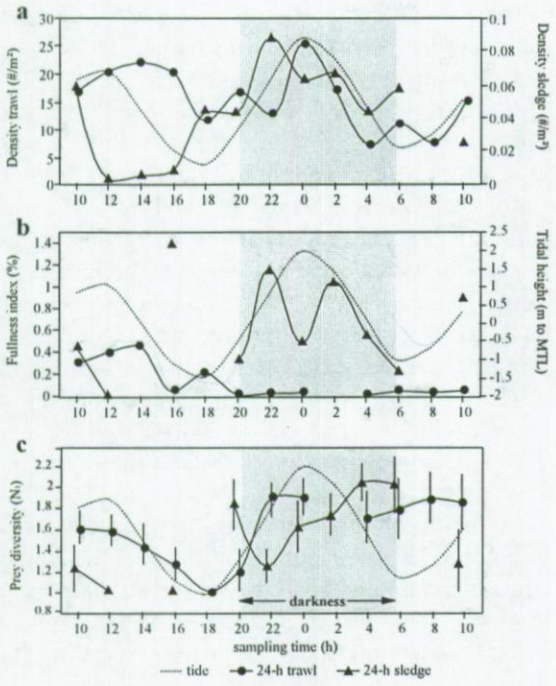

Fig. 8.3 Tidal curve and tidal-diurnal patterns in density (a), fullness index (b), and prey diversity (± standard error) (c) for shrimp caught during the 24-h surveys (brackish subtidal, 18-19 September 1991) with a 3-m beam trawl and a hyperbenthic sledge

From both 24-h surveys, twice as many males were examined, while more females were taken from the brackish sub- and intertidal surveys, surely in spring (and winter). As the individuals for the stomach content analyses were randomly selected from the subsamples, this probably reflects the actual sex-ratio of the total samples taken during the different surveys.

There were significant effects of sex on fullness for the 24-h trawl and seasonal brackish surveys, but not for the 24-h sledge, seasonal marine, or intertidal surveys (Table 8.2). The main source of variation in both significant tables arose from more, respectively less, males with few remains in the stomachs. The other models were not significant, as the proportion of stomachs within the 3 fullness categories was comparable between both sexes.

Significant effects of time of the day and tidal water height on stomach fullness were found for the 24-h trawl survey. More stomachs with many remains were analysed during daytime and the proportions of the three categories differed significantly between the 2h-samples, but not between day and night. The main source of variation in the tidal model was attributed to more S_F and less S_E around high water. The day-night model was the only significant model for the 24-h sledge survey, mainly attributed to the low number of S_F during the day.

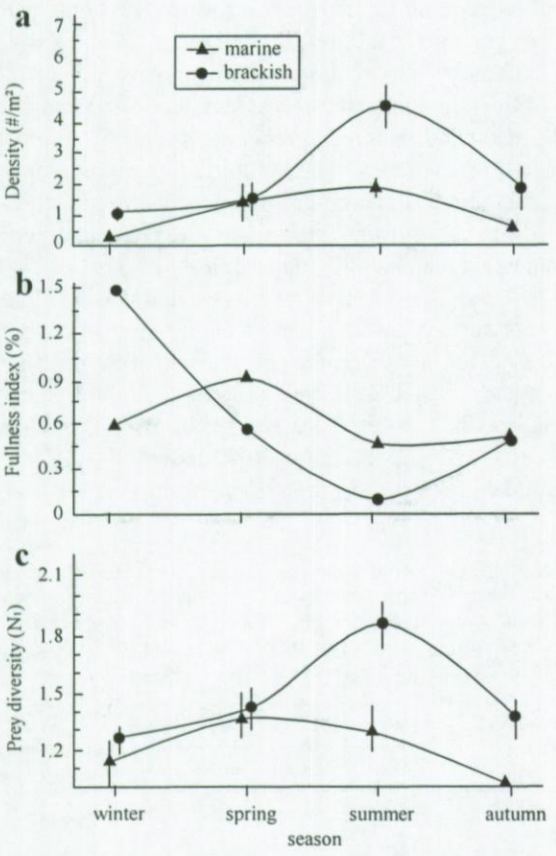

Fig. 8.2 Seasonal patterns in density (± standard error) (a), fullness index (b), and prey diversity (± standard error) (c) for shrimp caught in the marine and brackish subtidal parts of the Westerschelde (Sep'99 – May'00) with a 3-m beam trawl

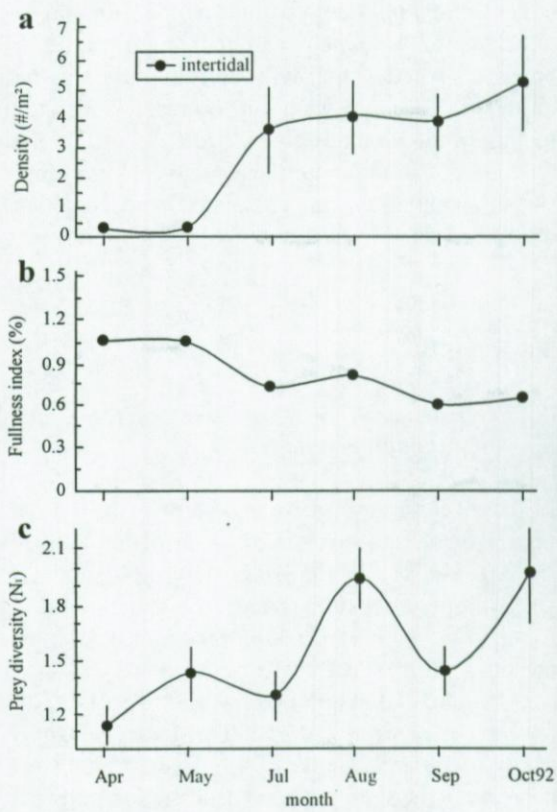

Fig. 8.4 Monthly patterns in density (± standard error) (a), fullness index (b), and prey diversity (± standard error) (c) for shrimp caught in the brackish intertidal part of the Westerschelde (Apr – Oct'92) with a 2-m beam trawl

For both the marine and brackish subtidal, significant effects of season on stomach fullness were found. In the brackish subtidal this was mainly attributed to more S_M and S_E, and less S_F in winter and vice versa in summer. For the marine subtidal, more S_M and no S_E were recorded in spring and vice versa in autumn.

The significance of the monthly model for the intertidal survey was mainly due to the variation in S_F between the months, and to more S_E and less S_M in spring. The spatial difference in stomach fullness between the brackish subtidal and intertidal subhabitats was mainly visible in the number of S_M, which was too low according to the expected frequency in the subtidal.

8.3.3 Fullness index

Fullness index (FI) followed a combined diurnal-tidal rhythm: FI was higher from dusk to dawn for shrimps taken in the 'hyperbenthal' (24-h sledge survey) with a clear tidal influence (0.3 at low water; 1.2 at high water), but with lowest feeding intensity at slack water, both at night and during the day (Fig. 8.3b). Also, around high water during daytime more food was present in the stomachs.

For shrimps taken in the epibenthal (24-h trawl survey), the diurnal pattern in FI was more or less opposite, with almost empty stomachs during the night. Still, a tidal pattern with more feeding around high water during the day was observed. All fullness indices were lower in the epibenthal, ranging between 0.1 and 0.5.

In the marine subtidal, FI was highest in spring (0.9), and more or less the same in the other seasons (0.5) (Fig. 8.2b). There was a decreasing trend in FI from winter (1.5) to summer (0.1) in the brackish subtidal.

No winter samples were taken in the brackish intertidal. Here, a decreasing trend in FI was noted from spring (1.1) to autumn (0.7) (Fig. 8.4b).

8.3.4 Trophic diversity

In total, 32 different prey categories were recorded from all stomachs, with a total of 1070 prey items from 719 stomachs (Table 8.3).

The diversity pattern in the diet of *C. crangon* from the 24-h trawl survey, more or less followed the tidal curve (Fig. 8.3c). Diversity (N_1) varied between 1.2 at low water and 1.9 at high water, but also higher values were found around low water at sunrise.

Diet diversity for the 24-h sledge survey (range 1.2 - 2.1) also followed the tidal curve, with a higher diversity during darkness, but seemed 2 hours out of phase.

Both in the marine and brackish subtidal, seasonal differences in prey diversity were small (Fig. 8.2c). Trophic diversity was lowest in the marine subtidal, with only 9 of the 32 prey categories present in the stomachs, and a little higher in spring-summer. In the brackish subtidal, prey diversity was 1.8 in summer and on average 1.3 for the other seasons.

Trophic diversity was highest in the intertidal, with 21 of the 32 prey categories present in the stomachs. No clear monthly pattern was seen, although prey diversity values were lower in spring-early summer (on average 1.3) and higher in sum-

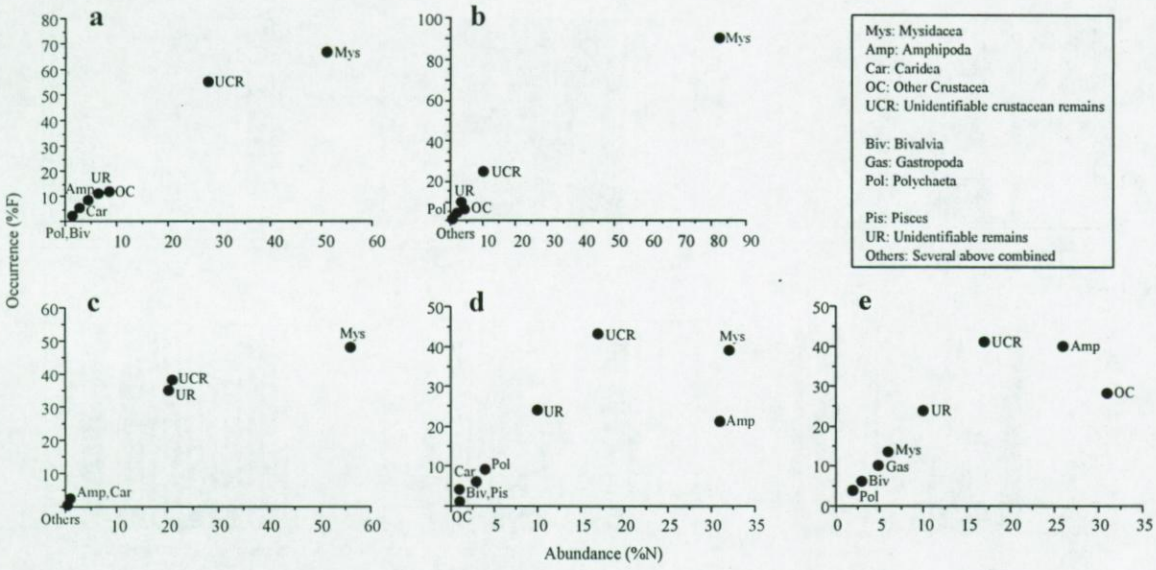

Fig. 8.5 Relative importance of the different prey categories in all non-empty stomachs of *Crangon crangon* for the different surveys: (a) 24-h trawl, (b) 24-h sledge, (c) marine subtidal, (d) brackish subtidal, (e) brackish intertidal. Note the different scales on both X and Y-axes

mer-early autumn (on average 1.8) (Fig. 8.4c).

8.3.5 Diet composition

The most important prey categories in terms of frequency of occurrence (%F, based on the non-empty stomachs) were mysids (on average >70 %F for the 24-h surveys and >40 %F for several seasons in the subtidal) and unidentifiable crustacean remains (on average 26-56 %F) (Fig. 8.5, Table 8.3). Amphipods were mainly present in the brackish sub- and intertidal stomachs (20-40 %F); unidentifiable remains were recorded in 10-35 %F of all non-empty stomachs.

Almost the same ranking of prey categories per survey was seen in terms of abundance and weight (Table 8.4), with an overall dominance of mysids (on average 32-82 %N and 22-79 %G of the non-empty stomachs) and unidentifiable crustacean remains (10-28 %N; 14-40 %G) in all surveys, except for the intertidal where mysids were replaced by other small crustaceans (calanoid and harpacticoid copepods mainly in May, cyprid larvae in August, and ostracods in August-September).

Numerically, the diet composition of *C. crangon* was supplemented with amphipods (mainly *Corophium* and a few *Bathyporeia* species) in the brackish sub- and intertidal (31 and 26 %N; 14 and 30 %G), and with unidentifiable remains in both the sub- and intertidal habitats (10-20 %N; 10-18 %G).

Shrimp cannibalism was generally low (highest in summer and autumn in the subtidal), and not observed intertidally. Predation on bivalves (mainly spat from at least three species), gastropods (mainly *Littorina* spat), polychaetes (mainly nereids), and fish, was low (<10 %F; <5 %N; <12 %G). Spat of the bivalve My*tilus edulis* was only observed in stomachs from autumn in the brackish subtidal and during daytime in the 24-h trawl survey. Most of the bivalve species that were preyed upon, were found in stomachs from the intertidal: *Abra* spat in July, *Cerastoderma edule* spat and juveniles in September, and *Mya arenaria* juveniles in October. Gastropods (mainly *Littorina* spat) were only recorded as prey in the intertidal (mainly October).

Several unidentifiable polychaete remains were present in the stomachs from the brackish subtidal, mainly in winter and spring, during daytime in the 24-h trawl survey, and during darkness in the 24-h sledge survey. Unidentifiable fish remains were only recorded in the brackish subtidal area throughout the year, and contributed most to the gravimetrical diet composition in winter.

8.3.6 Importance of mysids and difference in diet by size class

On average 1 mysid was recorded per non-empty stomach for both the 24-h and seasonal subtidal trawl surveys, and 2 mysids per non-empty stomach for the 24h-sledge survey (Table 8.3). These values were halved if all stomachs were taken into account. A maximum of 7 almost undigested mysids per non-empty stomach in the marine subtidal survey, and even up to 49 statoliths per stomach in the brackish subtidal were observed. Intertidally, mysids were only recorded sporadically in the shrimp stomachs.

During the 24-h trawl survey, only the stato-

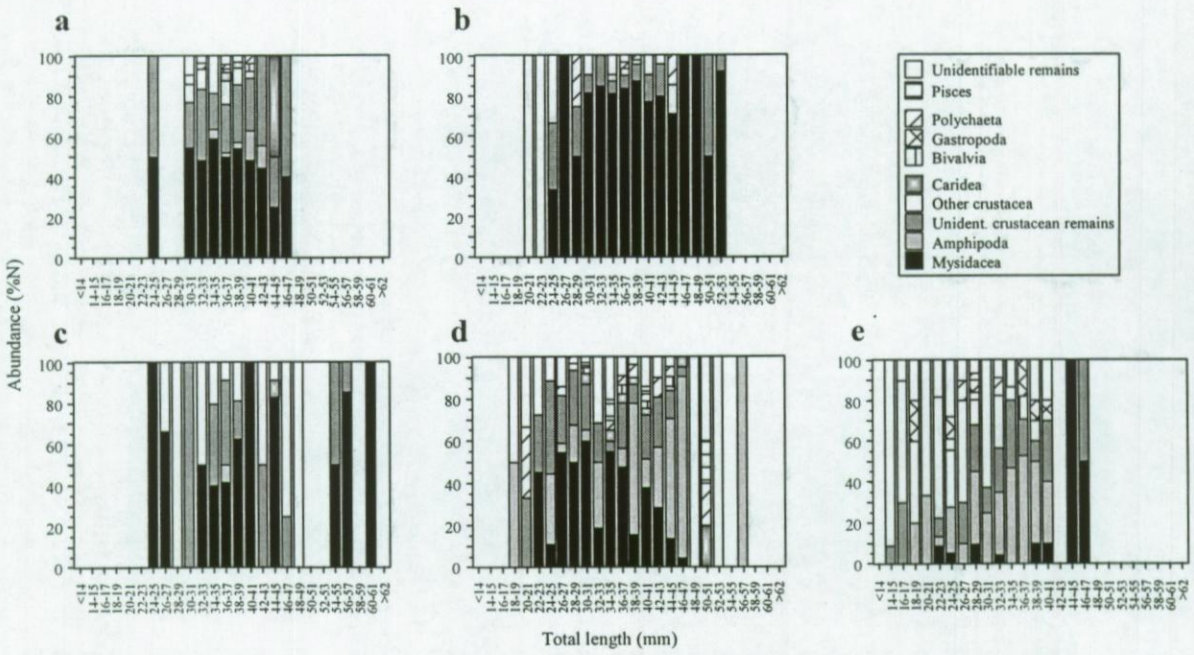

Fig. 8.6 Numerical diet composition per 2mm size class of *C. crangon* for the different surveys: (a) 24-h trawl, (b) 24-h sledge, (c) marine subtidal, (d) brackish subtidal, (e) brackish intertidal

Table 8.3 Preylist, average frequency of occurrence (%F) in non-empty stomachs per prey category, with minimum and maximum values per prey group and total number of prey categories per survey, average and maximum (between brackets) number of prey items per stomach per prey category and per survey

Taxon / prey category	Abbr.	Frequency of Occurrence					Average # prey items per stomach (+ maximum)				
		24-h		subtidal		intertidal	24-h		subtidal		intertidal
		trawl	sledge	marine	brackish	brackish	trawl	sledge	marine	brackish	brackish
Mysidacea	min-max	40-100	88-100	0-75	16-76	0-40					
Mysid Remains	MR	60	39	15	37	12	0.82 (4)	0.55 (4)	0.17 (2)	0.77 (7)	0.12 (1)
Neomysis integer	Neoint	12	50	-	2	1	0.13 (2)	0.67 (4)	-	0.03 (2)	0.01 (1)
Mesopodopsis slabberi	Messla	-	36	-	1	-	-	0.92 (6)	-	0.01 (1)	-
Gastrosaccus spinifer	Gasspi	-	-	29	-	-	-	-	0.69 (7)	-	-
Schistomysis kervillei	Schker	-	-	2	-	-	-	-	0.04 (2)	-	-
Schistomysis spiritus	Schspi	-	-	2	-	-	-	-	0.02 (1)	-	-
Gastrosaccus Larvae	GasLar	-	-	2	-	-	-	-	0.08 (4)	-	-
Mysidacea Larvae	MysLar	1	-	-	-	-	0.06 (6)	-	-	-	-
Amphipoda	min-max	0-50		0-6	5-41	23-67					
Corophium Species	CorSpe	-	-	-	21	27	-	-	-	0.78 (16)	0.46 (7)
Bathyporeia Species	BatSpe	3	-	-	1	6	0.03 (1)	-	-	0.01 (1)	0.09 (3)
Amphipod Remains	AR	5	-	2	-	7	0.05 (1)	-	0.02 (1)	-	0.07 (1)
Unidentifiable Crustacea	min-max	0-100	0-50	0-56	22-74	25-77					
Unident. Crustacean Remains	UCR	56	26	38	44	41	0.56 (1)	0.26 (1)	0.38 (1)	0.44 (1)	0.41 (1)
Caridea	min-max	0-25	0-7	0-6	0-12						
Crangon crangon	Cracra	5	1	2	6	-	0.05 (1)	0.01 (1)	0.02 (1)	0.06 (1)	-
Other Crustacea	min-max	0-20	0-13		0-3	0-54					
Copepoda Species	CopSpe	7	2	-	1	9	0.09 (3)	0.03 (2)	-	0.01 (1)	0.21 (5)
Cyprid Larvae	CypLar	3	3	-	-	6	0.05 (2)	0.03 (1)	-	-	0.27 (8)
Ostracoda Species	OstSpe	1	-	-	-	11	0.01 (1)	-	-	-	0.13 (2)
Harpacticoidea Species	HarSpe	-	-	-	1	4	-	-	-	0.01 (1)	0.12 (7)
Bivalvia	min-max	0-13	0-8		0-7	0-19					
Mytilus edulis Spat	MytSpa	2	-	-	2	-	0.02 (1)	-	-	0.02 (1)	-
Bivalve Remains	BR	-	1	-	1	2	-	0.01 (1)	-	0.01 (1)	0.02 (1)
Bivalvia Species	BivSpe	1	-	-	-	-	0.01 (1)	-	-	-	-
Abra Spat	AbrSpa	-	-	-	-	1	-	-	-	-	0.01 (1)
Cerastoderma edule	Ceredu	-	-	-	-	1	-	-	-	-	0.01 (1)
Cerastoderma Spat	CerSpa	-	-	-	-	1	-	-	-	-	0.01 (1)
Mya Arenaria	Myaare	-	-	-	-	1	-	-	-	-	0.01 (1)
Gastropoda	min-max					0-31					
Littorina Spat	LitSpa	-	-	-	-	7	-	-	-	-	0.1 (2)
Hydrobia Ulvae	Hydulv	-	-	-	-	1	-	-	-	-	0.01 (1)
Gastropoda Species	GasSpe	-	-	-	-	1	-	-	-	-	0.01 (1)
Polychaeta	min-max	0-15	0-13		0-25	0-10					
Polychaete Remains	PR	2	2	-	2	4	0.02 (1)	0.02 (1)	-	0.02 (1)	0.04 (1)
Nereidae Species	NerSpe	1	2	-	2	1	0.01 (1)	0.02 (1)	-	0.02 (1)	0.01 (1)
Annelida Species	AnnSpe	-	-	-	5	-	-	-	-	0.05 (1)	-
Pisces	min-max				0-6						
Pisces Species	PisSpe	-	-	-	4	0	-	-	-	0.04 (1)	-
Unidentifiable Remains	min-max	0-25	0-25	0-89	17-44	0-63					
Unidentifiable Remains	UR	10	8	35	24	24	0.1 (1)	0.08 (1)	0.35 (1)	0.24 (1)	0.24 (1)
Total # prey categories/items	32	15	11	9	16	21	1.99 (7)	2.61 (10)	1.77 (8)	2.51 (16)	2.39 (10)

liths of mysids remained in most of the stomachs. *Neomysis integer* occurred as 'complete' prey in 12 %F of the non-empty stomachs, mainly around high water during daytime (Table 8.3). Recalculated, mysids contributed 30-70 % both numerically and gravimetrically to the diet of these shrimps, with the lowest values around sunset (Table 8.4). All size classes of shrimps (25-48 mm L_t) had mysids and unidentifiable crustacean remains in almost the same proportions (Fig. 8.6a). No small other crustaceans (copepods) were recorded for shrimp >40 mm L_t.

For the 24-h sledge survey, mysid prey were more intact, with *Neomysis integer* occurring in 50 %F, *Mesopodopsis slabberi* in 35 %F, and unidentifiable mysid remains in 40 %F of all non-empty stomachs (Table 8.3). Mysids were almost the only prey contributing to the diet, both in terms of numbers and weight, 60-95 %N (and %G) during the night and 80-100 %N (and %G) during daytime (Table 8.4). This was the case for most shrimp size classes (24-53 mm), supplemented with a little more unidentifiable remains in the smaller length classes (<30 mm) (Fig. 8.6b).

In the marine subtidal, 3 other mysid species were preyed upon: *Gastrosaccus spinifer*, *Schistomysis spiritus* and *Schistomysis kervillei* occurred in respectively 30, 2 and 2 %F of the non-empty stomachs (Table 8.3). Mysids contributed most to the diet

Table 8.4 Number of stomachs analysed, numerical (%N) and gravimetrical (%G) diet composition (non-empty stomachs) of *C. crangon*, per prey category and sampling moment

Survey	stomachs	Mysidacea		Amphipoda		Caridea		Other Crust.		Unid. Crust.		Bivalvia		Gastropoda		Polychaeta		Pisces		Unid.Remains	
time/date	S_A (S_{NE})	%N	%G	%N	%G	%N	%G	%N	%G	%N	%G	%N	%G	%N	%G	%N	%G	%N	%G	%N	%G
24-h trawl (brackish - subtidal)																					
10:00	15 (11)	50	42	5	4	5	8	-	-	41	45	-	-	-	-	-	-	-	-	-	-
12:00	15 (11)	68	65	-	-	-	-	8	0.3	12	23	4	<0.1	-	-	-	-	-	-	8	12
14:00	15 (13)	50	40	9	6	-	-	5	1	23	40	5	2	-	-	9	11	-	-	-	-
16:00	16 (8)	50	33	-	-	-	-	-	-	40	56	-	-	-	-	-	-	-	-	10	11
18:00	15 (4)	50	70	50	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20:00	15 (5)	33	10	-	-	17	64	17	2	17	14	-	-	-	-	-	-	-	-	17	10
22:00	18 (10)	33	31	5	5	-	-	19	3	33	50	-	-	-	-	-	-	-	-	10	11
00:00	15 (13)	52	48	7	7	-	-	7	0.6	31	41	-	-	-	-	-	-	-	-	3	3
02:00																					
04:00	15 (4)	67	55	-	-	-	-	-	-	22	33	-	-	-	-	-	-	-	-	11	12
06:00	15 (10)	45	43	-	-	5	7	14	1	27	39	-	-	-	-	-	-	-	-	9	10
08:00	14 (8)	55	36	-	-	9	24	5	0.1	23	35	5	1	-	-	5	5	-	-	-	-
10:00	15 (7)	47	33	-	-	-	-	7	1	47	66	-	-	-	-	-	-	-	-	-	-
Average		**51**	**42**	**4**	**3**	**2**	**7**	**7**	**1**	**28**	**40**	**1**	**0.2**	**-**	**-**	**1**	**1**	**-**	**-**	**5**	**5**
24-h sledge (brackish – subtidal)																					
10:00	16 (8)	82	84	-	-	-	-	9	0.3	9	16	-	-	-	-	-	-	-	-	-	-
12:00	5 (1)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	100
14:00																					
16:00	9 (6)	100	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18:00																					
20:00	20 (12)	61	57	-	-	-	-	4	1	13	21	4	1	-	-	4	5	-	-	13	15
22:00	13 (8)	94	93	-	-	-	-	-	-	-	-	-	-	-	-	6	7	-	-	-	-
00:00	23 (11)	73	70	-	-	-	-	5	0.1	9	11	-	-	-	-	5	10	-	-	9	8
02:00	22 (14)	77	78	-	-	3	4	6	2	14	17	-	-	-	-	-	-	-	-	-	-
04:00	25 (14)	86	81	-	-	-	-	2	<0.1	11	17	-	-	-	-	-	-	-	-	2	2
06:00	27 (11)	79	73	-	-	-	-	-	-	18	26	-	-	-	-	4	2	-	-	-	-
08:00																					
10:00	19 (3)	100	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Average		**82**	**79**	**-**	**-**	**0.4**	**0.7**	**3**	**0.4**	**10**	**14**	**0.4**	**0.1**	**-**	**-**	**-**	**-**	**2**	**2**	**3**	**3**
Marine (subtidal)																					
2/09/1999	30 (17)	41	46	-	-	5	16	-	-	32	24	-	-	-	-	-	-	-	-	23	13
26/11/1999	15 (6)	-	-	-	-	-	-	-	-	33	40	-	-	-	-	-	-	-	-	67	60
17/02/2000	15 (9)	20	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	80	73
18/05/2000	16 (16)	79	67	2	3	-	-	-	-	19	31	-	-	-	-	-	-	-	-	-	-
Average		**56**	**49**	**1**	**1**	**1**	**6**	**-**	**-**	**21**	**25**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**20**	**18**
Brackish (subtidal)																					
2/09/1999	47 (42)	62	34	1	0.5	4	23	1	0.1	23	33	2	1	-	-	-	-	1	3	5	5
25/11/1999	48 (34)	8	7	61	29	2	12	1	0.2	10	21	1	7	-	-	-	-	-	-	16	24
16/02/2000	48 (32)	7	9	62	23	-	-	-	-	10	11	-	-	-	-	11	10	1	39	8	7
17/05/2000	45 (32)	30	28	11	16	4	2	-	-	26	28	2	0.2	-	-	11	10	4	4	13	11
Average		**32**	**22**	**31**	**14**	**3**	**12**	**1**	**0.1**	**17**	**25**	**1**	**2**	**-**	**-**	**4**	**4**	**1**	**12**	**10**	**10**
Intertidal (brackish)																					
2/04/1992	15 (10)	7	10	29	34	-	-	21	0.6	21	34	-	-	-	-	14	12	-	-	7	9
11/05/1992	15 (13)	-	-	11	12	-	-	61	17	26	67	-	-	-	-	3	5	-	-	-	-
9/07/1992	15 (12)	-	-	58	58	-	-	-	-	16	24	11	7	5	0.1	-	-	-	-	11	12
6/08/1992	15 (15)	13	10	15	26	-	-	46	2	21	50	-	-	-	-	2	4	-	-	4	7
7/09/1992	17 (16)	4	3	19	30	-	-	23	2	15	33	12	1	8	0.1	-	-	-	-	19	31
7/10/1992	16 (16)	6	7	39	29	-	-	12	2	8	21	2	1	14	0.2	-	-	-	-	20	40
Average		**6**	**5**	**26**	**30**	**-**	**-**	**31**	**4**	**17**	**39**	**3**	**1**	**5**	**0.1**	**2**	**3**	**-**	**-**	**10**	**17**

in spring (80 %N, 65 %G) and summer (40 %N, 45 %G). In all seasons, the rest of the diet consisted of unidentifiable (crustacean) remains, which actually could all stem from mysids (Table 8.4). Mysids were preyed upon in different proportions by most size classes (24-60 mm) (Fig. 8.6c).

In the brackish subtidal, most prey items were highly digested, and mysids were again mainly recorded as statoliths (40 %F), sometimes in high numbers (10-50 statoliths per stomach, mainly in summer) (Table 8.3). Mysids contributed around 10 %N (and %G) in autumn-winter and 60 %N (35 %G) in spring-summer. Mysids were found in shrimps of 22-47 mm, and were gradually replaced by amphipods (numerically) (Fig. 8.6d). In autumn and winter, the shrimp diet consisted of 60 %N amphipods, but the relative gravimetrical contribution of mainly *Corophium* species only amounted to 23 and 29 %G, respectively (Table 8.4). The latter prey category became more important than mysids for shrimps >38mm L_t. Gravimetrically, unidentifiable (crustacean) remains were more important in the size classes <30 mm; shrimp, fish and polychaetes in the length classes >30 mm.

Intertidally, mysids were less important prey (except for the few shrimps >40 mm), only occurring in 12 %F of the non-empty stomachs (Table 8.3). Numerically, other small crustaceans accounted for 10 to 60 %N of the diet composition (except in July), but only in May copepods were of some importance gravimetrically. Highest numbers of other small crustaceans were found in shrimp 15-40 mm, which were gradually replaced by amphipods (and unidentifiable crustacean remains) (Fig. 8.6e). Gravimetrically, am-

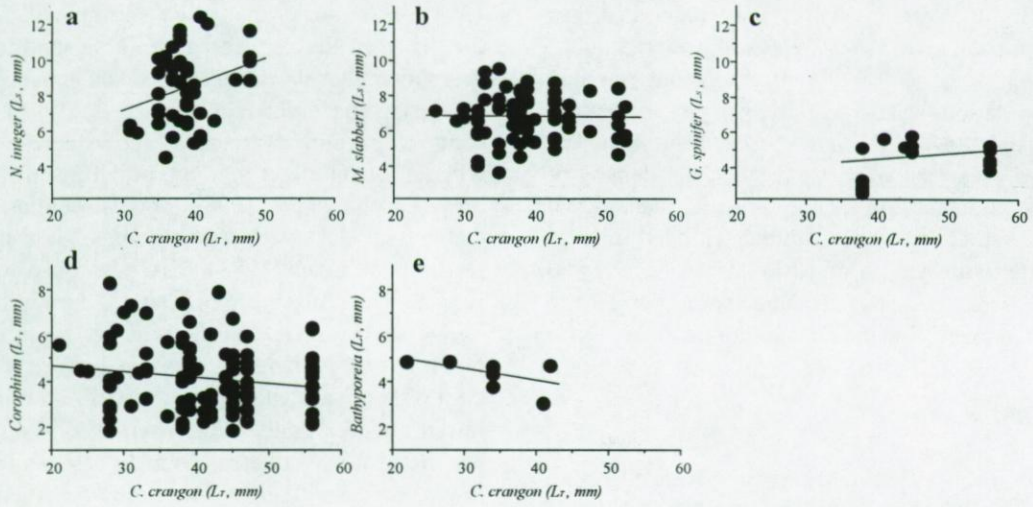

Fig. 8.7 Predator *Crangon crangon* versus prey length for 3 mysid species *Neomysis integer* (a), *Mesopodopsis slabberi* (b), and *Gastrosaccus spinifer* (c), and 2 amphipod species *Corophium* (d) and *Bathyporeia* (e) species, based only on almost 'undigested' prey-items from all stomach analyses (L_S, standard length; L_T, total length). None of the regressions were significant

phipods (mainly *Corophium* species, and *Bathyporeia* species in July), constituted 10-60 %G of the diet, supplemented with 20-70 %G unidentifiable crustacean remains and 10-40 %G unidentifiable remains throughout the sampled period (Table 8.4).

8.3.7 Predator versus prey length

Preyed *Neomysis integer* were 4.5-12.5 mm standard length (L_s), *Mesopodopsis slabberi* 3.7-9.5 mm L_s, and *Gastrosaccus spinifer* 2.5-5.8 mm L_s. Preyed *Corophium* species were 1.9-8.3 mm total length (Lt) and *Bathyporeia* species 3-4.9 mm L_t. No significant regressions could be established between shrimp and mysid or amphipod length (Fig. 8.7).

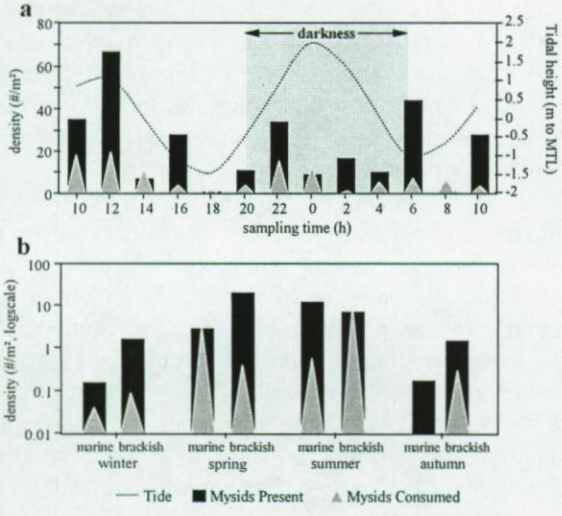

Fig. 8.8 Predation impact of *C. crangon* on the standing stock of the mysid populations for (a) the 24-h surveys, and (b) the seasonal marine and brackish subtidal surveys

8.3.8 Predation impact on mysid populations

The density pattern of all mysids, calculated from the 24-h sledge survey, more or less followed the tidal cycle with a peak of 67 ind m^{-2} at high water during the day, lowest values around low water (1 ind m^{-2}), and mid values during the night (Fig. 8.8a). During ebb tide 70-95 % of the mysids were *Mesopodopsis slabberi*, while during flood tide the ratio of *M. slabberi* and *Neomysis integer* was 1:1 (Muhando 1992 and this study). Only few individuals of *Gastrosaccus spinifer* and *Schistomysis spiritus* were recorded during the 24-h sledge survey.

During the 24-h survey, the shrimp predation pattern followed the density pattern of the mysids. The shrimp population consumed 10-50 % of the mysid standing stock per day. For 4 sampling times, the estimated predation impact exceeded mysid density.

In the period 1999-2000 mysid densities in the brackish subtidal were always an order of magnitude higher than in the marine subtidal, except in summer, due to exceptionally high average densities of *Mesopodopsis slabberi* in the marine part (Chavatte 2001). Mysid densities followed a seasonal pattern, with much higher densities in spring and summer, and on average 0.2-12 ind m^{-2} in the marine subtidal and 2-22 ind m^{-2} in the brackish subtidal. *Neomysis integer* was the commonest mysid species, mainly recorded from the brackish subtidal, with peak densities in spring. *Mesopodopsis slabberi* was recorded from both subareas, but not in winter, with much higher densities in the brackish zone, except in summer. Three mysid species were recorded mainly from the marine subtidal: *Gastrosaccus spinifer* (quite common in spring-summer), *Schistomysis kervillei* and *Schistomysis spiritus* (both in low densities

throughout the year). Only few individuals of *Praunus flexuosus* and *Siriella armata* were found.

On average 0-27 % of the mysid standing stock populations was consumed per day in the marine subtidal and 3-19 % in the brackish subtidal. The calculated predation impact exceeded the density of the mysid population in spring in the marine part and in summer in the brackish subtidal. This led to average consumption values of 10 to 35 % of the mysid standing stocks per day, the latter value taking into account the overestimated consumption values.

8.3.9 Consumption

Based on changes in daily ration from literature (formulas 1 and 2), shrimps from the Westerschelde consumed on average 11 % of their bodyweight (BW) per day during the 24-h trawl survey, up to 19 %BW during winter and on average 10 %BW in the other seasons in the subtidal, and about 17 %BW in the brackish intertidal.

Based on the stomach content analyses (formula 3), one shrimp on average consumed 7.4 and 6.2 mg ADW d^{-1} during the 24-h trawl and 24-h sledge surveys, respectively. Taking into account a feeding period of 8 hours per day in the epibenthal for the other surveys (formula 4), one shrimp on average consumed 7.1 and 10.3 mg ADW d^{-1} in the marine and brackish subtidal, respectively, and 6.6 mg ADW d^{-1} intertidally. Depending on whether stomach weight was based on real measurements or on recalculations prior to ingestion, *Crangon crangon* only consumed on average 0.6 to 4.9 % of their bodyweight per day during the 24-h trawl survey, 4.1 to 7.9 %BW d^{-1} during the 24-h sledge survey, 2.3 to 4.7 %BW d^{-1} in the marine subtidal, 1.2 to 6.8 %BW d^{-1} in the brackish subtidal, and 3.8 to 14.2 %BW d^{-1} intertidally (formula 5) (Table 8.1).

The latter values led to a daily consumption of minimum 0.01 and maximum 0.12 g ADW m^{-2} d^{-1} by the shrimp population for the 24-h trawl survey. With an 8-h feeding period, minimum and maximum yearly consumption values were 1.2-2.4, 1.4-7.9 and 2-7.4 g ADW m^{-2} yr^{-1} for the marine and brackish subtidal and brackish intertidal, respectively. With respective surface areas of 130, 40 and 14 km^2, the maximal yearly consumption by the shrimp population amounted to 316 tonnes ADW yr^{-1} in each subtidal part, and 103 tonnes ADW yr^{-1} on the brackish intertidal sandflats.

8.4 Discussion

8.4.1 Tidal - diurnal patterns

Density is related to locomotor activity and thus to feeding intensity (del Norte-Campos & Temming 1994). This means that more shrimp will likely be caught when they are foraging. On a sandy shore, it was shown that shrimps displayed an enhanced activity during the night (Burrows *et al.* 1994). On the contrary, shrimps were most active during the day without a tidal effect in a microtidal Swedish coastal area (Gibson *et al.* 1998). Several studies showed that brown shrimp *Crangon crangon* is a nocturnal feeder (*e.g.* Evans 1983). This was only partly the case for juvenile shrimps caught during the 24-h sledge survey in the Westerschelde. From the 24-h trawl and 24-h sledge surveys, it became clear that both density and feeding intensity of *C. crangon* followed a mixed tidal-diurnal rhythm. Shrimp activity was more tidally related, with highest densities and lowest number of empty stomachs recorded around high tide, while the shrimp population was more spread throughout the epibenthal (close to the bottom) and hyperbenthal (between 0 and 1 m above the bottom) water layers during the night. Also, Ansell *et al.* (1999) did not find distinct day-night differences on a Scottish sandy beach.

In a number of shallow microtidal marine areas in western Sweden, feeding peaks for *C. crangon* were recorded around dawn and dusk (Pihl & Rosenberg 1984). Contrastingly, both density and the number of non-empty stomachs in the epibenthal were lowest around the twilight hours in the Westerschelde. This coincided more or less with low water in September 1991. In the Westerschelde, fullness index and prey diversity showed a tidal pattern, with higher values around high water, but only during daytime in the epibenthal, and mainly during the night in the hyperbenthal. During the night, fullness index was almost nil in the epibenthal, while diet diversity remained high till a few hours after sunrise. The tidal effect was even clearer both during day and night for the 24-h trawl survey, if stomach weight prior to ingestion or percentage non-empty stomachs were plotted against tide. Also, in the German Wadden Sea, fullness index followed a tidal (out-of-phase) pattern, rather than a diurnal pattern (del Norte-Campos & Temming 1994). From the different studies, it can be concluded that the tidal effect on feeding intensity of *C. crangon* seems to be larger than the diurnal effect.

Fullness indices (and number of stomachs with many remains) were higher for shrimps taken in the hyperbenthal, than for shrimp sampled with a 3-m beam trawl in the brackish subtidal. Several studies have shown that *C. crangon* digests prey quite rapidly, between 1 and 2 hours for mixed prey (Pihl & Rosenberg 1984) and small plaice (Gibson *et al.* 1995). For the 24-h sledge survey, the average consumption per shrimp, recalculated as prey weight prior to ingestion, more or less agreed with what was really found in the stomachs, but there was a large discrepancy between both consumption estimates for the 24-h trawl survey. During the latter survey,

mainly statoliths of mysids were found. Additionally, prey selection was dominated by mysids (and unidentifiable crustacean remains) for both 24-h surveys. This suggests that foraging mainly took place in the hyperbenthal layer, where mysids are the main component in the Westerschelde (Mees *et al.* 1993a). Probably, the shrimp caught in the epibenthal during the night were individuals not foraging in this higher water layer. The hyperbenthos concentrates near the bottom during daytime (Mees & Jones 1997). This could explain why fullness indices in the epibenthal were higher during daytime, as shrimp could forage on these hyperbenthic organisms closer to the bottom. Although, during daytime more bottom-related organisms (*e.g.* polychaetes, bivalves and shrimps), were preyed upon as well.

As the fullness indices were rather low for the 24-h trawl survey, the daily consumption based on the minimum calculations, is likely to be underestimated. The average value of 0.6 %BW was an order of magnitude lower than the one calculated with daily rations from literature (van Lissa 1977), or those found for other systems (*e.g.* Pihl & Rosenberg 1984). In the German Wadden Sea, daily ration was estimated at 16 %BW (del Norte-Campos & Temming 1994). The 'correct' daily consumption values for the Westerschelde will probably be somewhere in between the minimum and maximum estimates, and should only be based on recalculations for 'undigested' prey items. Furthermore, the daily consumption will probably be a combination of both 24-h surveys, i.e. a summation of day-feeding as found in the epibenthal and night-feeding as recorded for the hyperbenthal. Still, such values will be lower in the Westerschelde than most values found in literature. This could mean that mysids are energetically more important prey items than for example macrobenthic prey.

8.4.2 Seasonal - spatial patterns

From the 24-h surveys it was clear that highest fullness indices in the epibenthal were recorded during daytime. For the seasonal and monthly surveys, average fullness indices were comparable with those found in the 24-h sledge survey. A few stomach analyses of shrimp taken with the hyperbenthic sledge during the seasonal surveys (not presented), did not differ much from the ones taken with the beam trawl. As all seasonal and monthly surveys were performed during daytime, it was concluded that individuals taken with a beam trawl were representative for the seasonal feeding patterns of *Crangon crangon*.

Both seasonal and spatial patterns were observed in density, stomach fullness, diet composition and consumption. Significant differences in stomach fullness were recorded between the brackish sub- and intertidal. The model predicted more full stomachs in the subtidal than were actually found. This was probably related to the low fullness index in summer in the subtidal, which can partly be explained by the fact that all stomachs from the summer survey were taken from ebb-tide samples (Table 8.1). As was shown by the 24-h surveys there was a clear tidal influence on feeding intensity. Similarly, the seasonal differences in stomach fullness could be related to the moment of sampling. In all subhabitats, high fullness indices were recorded in spring (all flood-tide samples). In the brackish subtidal, higher fullness indices were calculated during winter (flood tide samples), while in the marine subtidal, low S_M and high S_E were observed in autumn (and winter), corresponding with slack low (and high) water, respectively.

However, tidal influence can only partly explain the observed differences. In Port Erin Bay (UK), shrimps were equally more feeding in winter (Oh *et al.* 2001). In both brackish sub- and intertidal habitats more juvenile shrimps were present during summer-early autumn. In the Severn estuary (UK) numbers peaked between summer and autumn, due to the arrival of young shrimps (Bamber & Henderson 1994). Growth rates of 0.12-0.35 mm d^{-1} were calculated for *C. crangon* (Kuipers & Dapper 1984). To achieve this fast growth, shrimp have to feed more intensively, which was reflected in the higher daily consumption rates during summer-autumn (mainly in the intertidal).

Differences in daily rations between experimental data and field observations were noted. Most studies on daily rations take into account a continuous feeding at a constant rate, with a constant evacuation rate (Evans 1984). For the present study, a daily feeding period of 8 hours was taken for the seasonal and monthly surveys, comparable with two feeding peaks around high water. The real daily consumption will probably be somewhere in between. Additionally, both minimum and maximum consumption estimates were presented, either based on the real weight of the stomachs or on the recalculated weight of the prey items prior to ingestion. For the 24-h surveys, these maximum values will be overestimations, but for the other surveys the maximum values are considered the 'best' estimates of daily consumption. Although, large differences were calculated in yearly consumption per m^2 for the marine and brackish subtidal, the total maximum yearly consumption by the whole shrimp population was comparable (316 tonnes ADW yr^{-1}) for both subtidal areas. No subtidal data on juvenile shrimp from other areas were found. The maximum intertidal consumption in the Westerschelde was 7.4 g ADW m^{-2} yr^{-1}. This was comparable with the average food consumption (6.7 g ADW m^{-2} yr^{-1}) of the juvenile shrimp population in the tidal zone of the western Wadden Sea (Kuipers & Dapper 1981).

Also, diet composition for *C. crangon* showed spatial and seasonal patterns. In the Westerschelde, postlarval shrimp are mainly present in the intertidal saltmarsh creeks, where they feed on amphipods and polychaete tail-ends (Cattrijsse *et al.* 1997). After a few weeks, these postlarvae have grown into the first juvenile length class, leave the creeks, and continu their early life history on the intertidal flats. Intertidal shrimps were on average 10 mm smaller than in the subtidal. From the numerical diet composition in the intertidal, it was clear that the smallest shrimp length classes mainly preyed upon calanoid copepods and gradually shifted to more amphipods. On the intertidal flats in the adjacent Oosterschelde, small shrimp (20 mm) mainly preyed upon copepods and unidentifiable remains (Boddeke *et al.* 1986). At a length >40 mm L_t, shrimps were mainly recorded from the subtidal, although smaller shrimp were present in this subhabitat as well. In the Wadden Sea smaller shrimp (<25 mm L_t) were restricted to the tidal zone, and spatially separated from the juveniles in the subtidal (Janssen & Kuipers 1980). No other studies directly compared shrimp stomach contents from both the sub- and intertidal. Prey availability may be influenced by substratum type (Pihl & Rosenberg 1984, Boddeke *et al.* 1986). In the Westerschelde, the sediment of the intertidal flat is a mixture of silt and sand, which was reflected in the higher diversity of different bottom-dwelling organisms in the shrimp diet.

In the subtidal part of the Westerschelde, mysids were an important prey category, more or less independent of shrimp-body size in the marine part, but gradually replaced in terms of numbers by amphipods with increasing predator size in the brackish subtidal. Oh *et al.* (2001) showed that size of invertebrate prey (mysids and amphipods) increased with body size of the shrimp. This was not the case for 3 mysid and 2 amphipod prey species in the Westerschelde. The shift from mysids to amphipods in the brackish subtidal was seasonally influenced, with more mysids taken during the warmer seasons and more amphipods during autumn and winter. In the Westerschelde, this coincided with higher densities of both prey categories, respectively. Average mysid densities were higher in spring and summer (Chavatte 2001), while densities of *Corophium* and *Bathyporeia* were higher in autumn and winter (Ysebaert 2000). Also, on mudbanks in the Loire estuary (France), *Neomysis integer* was mainly preyed upon in spring and summer (Marchand 1981). Predation on the different mysid and amphipod species clearly reflected the spatial distribution of the commonest prey species. In the marine subtidal, mainly *Gastrosaccus spinifer* (and both *Schistomysis* species) were preyed upon, while in the brackish subtidal, shrimp mainly took *Neomysis integer* and *Mesopodopsis slabberi*, the dominant mysid species in this subarea (Mees *et al.* 1993a, Mees 1994). *Corophium* and *Bathyporeia* species are typical brackish species (Cattrijsse *et al.* 1993), and were only preyed upon in the brackish subhabitats, although both amphipod species were more common intertidally (Ysebaert *et al.* 1998). Typical amphipod species from the subtidal, *Gammarus* species, were not selected as prey by *C. crangon*.

Sexual differences were of limited importance to the feeding activity of *C. crangon*. Only in the brackish subtidal (seasonally and diurnally), stomach fullness was significantly different between sexes. Most females analysed from the Westerschelde did not carry eggs. Also, in Port Erin Bay (Isle of Man), no differences were found in stomach fullness between males and non-ovigerous females (Oh *et al.* 2001).

8.4.3 Importance of mysids in the diet of Crangon crangon

Analysing the diet was rather difficult, as the prey items were highly crushed in many stomachs. Probably shrimp use sand grains to grind the prey items, as 70-90 % of the non-empty stomachs contained sand grains from a few to several hundreds per stomach. In the Loire estuary (France), sediment was considered an extra source of micro-organisms as food in the diet of *C. crangon* (Marchand 1981). Furthermore, unidentifiable crustacean remains and other unidentifiable remains were recorded in 40 and 20 % of the stomachs, respectively. The large number of empty stomachs (36 %) was also found in other studies (*e.g.* Pihl & Rosenberg 1984, Oh *et al.* 2001). Although evacuation rates may be high (*cf.* the many empty stomachs), hard parts (like statoliths) remain for a longer period in the stomachs (*cf.* the high number of stomachs with few remains). Even by taking into account the statolith-conversion rule (see the material and method section), this might have led to an overestimation of mysids in the different indices. However, almost undigested mysids were present as well in the stomach contents of the different surveys (up to 4 and even 7 'complete' prey per stomach). The high frequency of occurrence, and the high values in terms of numbers and weight, proved the importance of mysids in the shrimp diet, even in the marine part, where mysid densities were 5 to 10 times lower than in the brackish subtidal (see also Mees *et al.* 1993b).

The success of many estuarine (fish) species is dependent on their ability to exploit a wide variety of food items (de Sylva 1975). Also, the diet of brown shrimp in the Westerschelde was diversified. This study confirms the opportunistic feeding behaviour of *C. crangon*, as no significant differences in trophic diversity were recorded (except for the higher value in winter in the brackish subtidal). Still, small crustaceans were the main prey of *C. crangon*. Next to mysids, amphipods were important prey items in

the Westerschelde, the latter mainly in the brackish subhabitats. Together these two prey categories constituted >50 % and even up to 80 %, both in terms of occurrence and abundance, of the shrimp diet in the subtidal Westerschelde. These values will even be higher, as probably most of the crustacean and unidentifiable remains were equally derived from either mysids or amphipods. In a parallel food study of the demersal fish fauna, it was shown that amphipods and other epifaunal organisms were more vulnerable to be preyed upon during their excursions into the hyperbenthic water layer (Chapter 7). As such, amphipods like *Corophium* and *Bathyporeia* could also be regarded as 'hyperbenthic' organisms. In Port Erin Bay (UK), both mysids and amphipods accounted for >60 % of the shrimp diet, both in terms of occurrence and abundance (Oh *et al.* 2001). For the Humber estuary (UK) it was shown that gammarids and mysids formed the dominant prey of most fish species (Marshall 1995). In a Swedish coastal area, *C. crangon* (and shore crab *Carcinus maenas*) could reduce the estuarine population of *Corophium volutator* by >50 % (Pihl 1985).

The present study proves the importance of 'hyperbenthic' organisms in the diet of *C. crangon*. As already shown, mysids were very abundant in the subtidal, while macrobenthic epi- and infaunal organisms were more common intertidally (Ysebaert *et al.* 1993, Ysebaert 2000). This is reflected in the diet, as mysids were less important prey in the intertidal. However, most studies on the feeding ecology of *C. crangon* were based on intertidally sampled shrimps. This is probably the main reason why these studies found 'endobenthic' organisms to be the most important component of the diet. In a shallow Swedish coastal area, smaller shrimp mainly preyed upon harpacticoid copepods, while larger shrimp were more dependent on bivalves, polychaetes, and crustaceans, the latter mainly present in the modal length classes of the shrimp population (Evans 1983). In the lower Severn estuary (UK), shrimps fed on annelids, molluscs and small crustaceans, while no mysids were taken (Henderson *et al.* 1992). In the German Wadden Sea, mainly amphipods, polychaetes and foraminiferans were preyed upon (del Norte-Campos & Temming 1994). In contrast to several studies, few fish remains were found in the stomachs from the Westerschelde. Although it was shown that mainly larger shrimps preyed upon small (postlarval) fish species (van der Veer & Bergman 1987, Gibson *et al.* 1995). As was found in other studies, shrimp cannibalism was low (*e.g.* del Norte-Campos & Temming 1994).

Most studies did find mysids in the shrimp diet, but these were less important than the epifaunal or infaunal organisms (*e.g.* Marchand 1981, Raffaelli *et al.* 1989, del Norte-Campos & Temming 1994, Pihl & Rosenberg 1984). It is clear that spatial and temporal availability of the different prey organisms are important factors affecting the diet of *C. crangon*. In tidal puddles and in the surfzone of a Belgian sandy beach, juvenile shrimp mainly fed on mysids and amphipods (Stuer 2002). Preliminary stomach content analyses from the subtidal part of the adjacent Oosterschelde, mainly showed bivalve and polychaete remains, next to some crustacean remains (Hostens, unpubl. data). In contrast with the Westerschelde, the Oosterschelde is dominated by macrobenthic organisms (Meire *et al.* 1991) and mysids are much less abundant (Mees & Hamerlynck 1992, Chavatte 2001).

Interspecific competition between fish and macro-crustaceans has been shown by means of niche overlap (Pihl 1985, del Norte-Campos & Temming 1994, Oh *et al.* 2001). As both demersal fishes and shrimps are opportunistic predators, niche overlap will probably be high in the Westerschelde, as well. In a previous study, it was shown that the commonest demersal fishes were important predators of the hyperbenthos and of mysids in particular, but the fish populations only consumed on average 1% of the mysid standing stocks per day (Chapter 7). *C. crangon* is on average 4 to 7 times more abundant than the whole fish population in the Westerschelde (Chapter 2). Juvenile shrimps are not efficiently sampled with a hyperbenthic sledge, due to the small frame and mesh size. Therefore, predation impact on mysids was based on shrimp densities caught with the beam trawl. The shrimp population consumed on average 10 to 35 % of the mysid standing stocks per day in the marine and brackish subtidal. Taking into account a P/B ratio of 6 (Mees *et al.* 1994), the yearly production of all mysids amounted to 0.15 and 0.26 g ADW m^{-2} yr^{-1} in both subhabitats, respectively. These values were in the same range as the values for *Neomysis integer* in the brackish part of the Westerschelde (Mees *et al.* 1994). With maximum yearly consumption values of 2.4 and 7.9 g ADW m^{-2} yr^{-1}, and mysids constituting on average 35 and 20 % of the gravimetrical diet, shrimps should have consumed 0.8 and 1.6 g ADW m^{-2} yr^{-1} of the mysid production in the marine and brackish subtidal, respectively. The large discrepancy (an order of magnitude difference) between mysid production and shrimp consumption was probably related to net efficiency problems. If the beam trawl was more efficient and the hyperbenthic sledge less efficient than usually considered, both mysid production and shrimp consumption values will converge towards each other. Irrespective of the conversion problems, the present study showed that mysids are important prey, and the predation impact of the brown shrimp on the mysid population was high in the subtidal Westerschelde.

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Appendix 1 Allometric regressions, length-weight regressions (natural logarithms) and assigned weight values, used in the stomach analyses to recalculate prey length and weight prior to ingestion. Length (L) and diameter (D) in mm, weight (W) in mg ashfree dry weight. L_s standard, L_t total, L_{tel} telson, L_{urp} uropod, L_{urs} urosome, L_{car} carapace, L_{anp} antennal plate, L_{ant} first antenna, L_{as2} second segment first antenna, D_{stl} statolith

taxon/species	Regression	Source
Mysidacea		
Gastrosaccus spinifer	$L_s = -1.457 + 9.175\ L_{tel}$ (n=8; r^2=0.90)	This study
	$L_s = -1.499 + 9.988\ L_{urp}$ (n=8; r^2=0.90)	This study
	$L_s = -4.943 + 147.996\ D_{stl}$ (n=8; r^2=0.95)	This study
	$L_s = 1.048 + 2.32\ L_{car}$ (n=118; F=325)	Hostens 1989
	$\ln W = -5.896 + 2.876 \ln L_s$ (n=118, F=721)	Hostens 1989
Mesopodopsis slabberi	$L_s = -1.438 + 15.518\ L_{tel}$ (n=10; r^2=0.92)	This study
	$L_s = -1.707 + 8.975\ L_{urp}$ (n=10; r^2=0.92)	This study
	$L_s = 0.135 + 46.341\ D_{stl}$ (n=10; r^2=0.86)	This study
	$\ln W = -6.107 + 2.876 \ln L_s$	Mees 1994
Neomysis integer	$L_s = -0.387 + 5.9\ L_{tel}$ (n=10; r^2=0.92)	This study
	$L_s = -2.759 + 7.913\ L_{urp}$ (n=10; r^2=0.93)	This study
	$L_s = -3.982 + 75.64\ D_{stl}$ (n=10; r^2=0.80)	This study
	$L_s = -1.650 + 3.759\ L_{car}$ (n=112; r^2=0.91)	Mees et al. 1994
	$L_s = 0.478 + 3.49\ L_{anp}$ (n=10; r^2=0.99)	This study
	$\ln W = -5.539 + 2.267 \ln L_s$ (n=100, r^2=0.99)	Mees et al. 1994
Schistomysis Species	$L_s = -0.904 + 5.728\ L_{tel}$ (n=8; r^2=0.97)	This study
	$L_s = -1.405 + 6.741\ L_{urp}$ (n=8; r^2=0.97)	This study
	$L_s = -0.665 + 42.28\ D_{stl}$ (n=8; r^2=0.96)	This study
	$L_s = 0.510 + 2.990\ L_{car}$ (n=190; F=1779)	Hostens 1989
	$L_s = 0.005 + 5.051\ L_{anp}$ (n=8; r^2=0.95)	This study
	$\ln W = -5.898 + 2.931 \ln L_s$ (n=190, F=3061)	Hostens 1989
Amphipoda		
Corophium Species	$L_t = 4.949 + 1.768\ L_{urs}$ (n=10; r^2=0.91)	This study
	$L_t = 5.696 + 0.219\ L_{ant}$ (n=10; r^2=0.94)	This study
	$L_t = 5.605 + 0.717\ L_{as2}$ (n=10; r^2=0.97)	This study
Gammarid amphipods	$\ln W = -5.857 + 2.863 \ln L_t$ (n=124, F=2498)	Hostens 1989
Caridea		
Crangon crangon	$L_t = 3.283 + 4.982\ L_{tel}$ (n=163; r^2=0.94)	This study
	$L_t = 3.765 + 2.906\ L_{car}$ (n=163; r^2=0.97)	This study
	$\ln W = -12.724 + 2.863 \ln L_t$ (n=165, r^2=0.96)	This study
Other Crustacea		
Calanoida Species	0.089	Beyst et al. 1999
Cyprid Larvae	0.014	Hostens 1989
Harpacticoidea Species	0.002	Hamerlynck et al. 1986
Ostracoda Species	0.014	Hamerlynck & Cattrijsse 1994
Mollusca		
Bivalvia Spat (& Gastropoda Spat)	$\ln W = -4.052 + 2.817 \ln L$	Govaere 1978
Polychaeta		
Nereidae Species	$\ln W = -7.139 + 2.489 \ln L$	Govaere 1978
Pisces		
Pisces Species (from *Pomatoschistus minutus*)	$\ln W = -7.851 + 3.460 \ln L_s$	Hamerlynck et al. 1986

CHAPTER 8 - ADDENDUM THE WESTERSCHELDE ESTUARY: TWO FOOD WEBS AND A NUTRIENT RICH DESERT

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Abstract. *Hummel et al. (1988b) hypothesised the concomitant existence of two separate food chains in the Westerschelde: a photo-autotrophic coastal food chain in the marine part and a heterotrophic chain in the brackish part. The present study intends to re-examine the hypothesis on the basis of recently published data. Biomass gradients of the important functional units along an estuarine transect were observed to differ from those reported by Hummel et al. (1988b) in some important aspects. The bimodal primary production gradient reported by van Spaendonk et al. (1993) does not resemble the phytoplankton biomass curve, gradually increasing from the sea to Antwerp proposed by Hummel et al. (1988b). Estimates of mesozooplankton biomass were found to be about an order of magnitude lower than reported by Hummel et al. (1988b) and to display a completely different and more complex spatial pattern. However, the new gradient found is more in line with the hypothesis of two food chains than the gradient reported by Hummel et al. (1988b). In the macrobenthos the biomass peak in the brackish part reported by Hummel et al. (1988b) could not be confirmed. This finding does not falsify the original hypothesis as the function of this detritus dependent macrobenthic fauna is largely taken over by the hyperbenthic mysids, a group of previously unknown importance in the system. The existence of two food chains is also supported by the gradients observed in fish and epibenthic invertebrates, functional units not addressed by Hummel et al. (1988b). In the zone between the two different food chains the dominant animal groups of the pelagic system have only a low biomass, this is the nutrient rich desert of the title. The zone upstream of the Dutch-Belgian border supports no hyperbenthos, no epibenthos and no mesozooplankton because of the low dissolved oxygen concentrations (less than 40 % saturation), but there is a prominent peak in the microzooplankton. Clearly, in the brackish part, the richness of most functional units can only be explained on the basis of an input of organic matter from outside, consumed through a heterotrophic food chain. A second, smaller peak is observed close to the mouth of the estuary and is dependent on the primary production in the marine part of the estuary. Even for individual species this clear bimodal pattern can be observed. This disqualifies simplistic physiological models of estuarine succession as a basis for the findings. In the oxygenated part of the system there is no good general correlation between macrobentic biomass (mostly suspension-feeders) and primary production. Macrobenthic biomass is highly variable in this zone, probably as a result of local differences in current velocity maxima. The new data confirm the view of Hummel et al. (1988b) but it is concluded that these authors must have formulated their hypothesis intuitively and could not have done so from the data available at the time.*

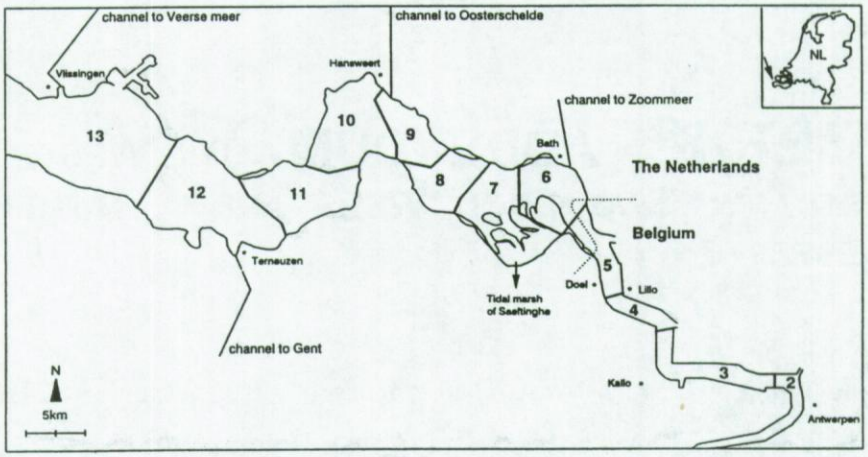

Fig. 8.9 Map of the study area with a division in 12 compartments according to the MOSES model (Soetaert *et al.* 1992)

8.1 Introduction

There has recently been renewed emphasis on food web theory in ecological studies (Lawton 1989). Much of the thinking on this subject has been severely hampered by the lack of appropriate data on enough components of reasonably complex food webs. The claim by Briand & Cohen (1987), that food chains in two-dimensional areas such as estuaries tend to be shorter, was not confirmed by a recent, relatively well documented, study of an estuarine food web (Hall & Raffaelli 1991). However, in studies of the properties of food webs (*e.g* chain length, degree of omnivory, connectance, etc.) of a large area encompassing a diversity of habitats, such as an estuary, care should be taken not to confound different food chains or "compartments" *sensu* Paine (1980). Besides the theoretical aspects of compartmented webs regarding system stability (Pimm & Lawton 1980), the elucidation of web infrastructure is a prerequisite for a correct evaluation of web properties (Raffaelli & Hall 1992).

With the increased research effort into the dominant role of bacteria in secondary production in marine and estuarine ecosystems (Cole *et al.* 1988) more insight has been gained into the distinction between detritus based food chains, termed heterotrophic (Smith *et al.* 1989, Findlay *et al.* 1991), where respiration exceeds production and phytoplankton dominated food chains, termed autotrophic, where primary production exceeds respiration. Unlike previously thought, the bacterial production does not simply result in a remineralisation of nutrients but also opens up a loop towards the zooplankton through the protozoans (Billen *et al.* 1990). In estuarine systems it is thought this loop may support an important food chain sustained by the detrital organic carbon imported from the riverine system. Care should be taken with the term autotrophic food chain as around hydrothermal vents, methane sources, hypoxic parts of estuarine systems and elsewhere chemo-autotrophic food chains exist (*e.g* Conway & McDowell 1990). Photo-autotrophic would be a better term for the food chains termed autotrophic by Findlay *et al.* (1991).

Hummel *et al.* (1988b) hypothesised the concomitant existence of two separate food chains in the Westerschelde. Their hypothesis was based on scattered and comparatively old data from the literature. In the meantime a concerted research effort has been developed by Dutch and Belgian scientists which has begun to make available more systematically collected and more reliable recent data for different functional units (phytoplankton, zooplankton, hyperbenthos, etc.) of the Westerschelde ecosystem. These data are now being used for the development and validation of an ecological model of the Westerschelde (Soetaert *et al.* 1992, P.M.J. Herman et al., unpublished). This paper will examine some of the input data for this model in relation to the Hummel *et al.* (1988b) hypothesis. Additional data on the higher trophic levels in the Westerschelde, not to be included in the MOSES model are also presented.

8.2 Materials and Methods

The Westerschelde estuary (Fig. 8.9) is the lower part of the river Schelde. It is the last remaining true estuary of the Delta area and is characterized by a marked salinity gradient. The estuarine zone of the tidal system extends from the North Sea (Vlissingen) to Antwerp, 80 km inland. Further upstream the system can be termed riverine, though the tidal influence extends to Gent. The water in the estuarine part is virtually completely mixed and the residence time in the brackish part is rather high: about 60 days (Soetaert & Herman 1995b). Consequently fresh water (average inflow 100 $m^3 s^{-1}$) dilution is gradual and

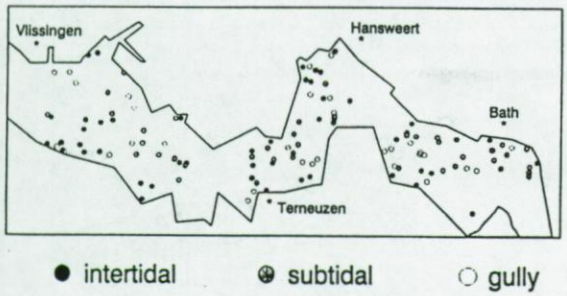

Fig. 8.10 Sampling grid of the macrobenthos data in the Westerschelde

downstream transport is relatively slow. Shifts in salinity zone distribution occur in accordance with seasonal variations in the freshwater inflow. The abiotic environment is discussed in Heip (1989b) and Van Eck *et al.* (1991). The estuary carries high pollution loads, both in anorganic and organic contaminants. The riverine part is anoxic throughout most of the year (Herman *et al.* 1991).

Spatially the estuarine system under consideration in the present study was divided into 12 compartments according to the MOSES model (Soetaert *et al.* 1992). The MOSES model contains an extra compartment in the riverine system. Therefore the 12 estuarine compartments are numbered 2 to 13 when going from Antwerp to the North Sea (Fig. 8.9). Functionally the units considered are phytoplankton (van Spaendonk *et al.* 1993), zooplankton comprising mesozooplankton, benthic larvae and part of the microzooplankton, ie. Rotatoria and *Noctiluca miliaris* (Soetaert & Van Rijswijk 1993), macrobenthos (Craeymeersch *et al.* 1992), hyperbenthos (Mees & Hamerlynck 1992, Mees *et al.* 1993b), epibenthos and fish (Chapter 2-Add.2). The reader is referred to these publications for detailed descriptions of the sampling methodologies. Table 8.5 shows a matrix of the spatial compartments and the functional units for which data were available.

The primary production data are based on fortnightly measurements taken in 1989 (van Spaendonk *et al.* 1993). The zooplankton data are annual means from approximately fortnightly samples from April 1989 through March 1991 (Soetaert & Van Rijswijk 1993). The macrobenthos data refer to a stratified random sampling in the autumn of 1990 according to the grid shown in Fig. 8.10. The strata were intertidal, subtidal and gully (more than 10 m below Mean Tidal Level) stations. During the macrobenthos survey no data were collected upstream of compartment 6, but it is known that in the upstream (hypoxic) zone only some oligochaetes survive (P.M. Meire, pers. comment). For the hyperbenthos the data are the averages per station of the 1990 seasonal data reported in Mees *et al.* (1993b). The area upstream of compartment 6 was explored for hyperbenthos in March, April and May 1990 and in August 1991 but no animals were found. The epibenthos and fish data are annual means based on monthly samples collected in 1989. The data in compartments 4 and 5 refer to samples collected from the intake screens of Doel power station. Between April and July virtually no fish were recorded in this area (P.A. van Damme, unpublished data).

Values reported as Ash-free Dry Weight (ADW) were converted to g C using the same 0.4 conversion factor as in Hummel *et al.* (1988b). Dry weight from the zooplankton study (Soetaert & Van Rijswijk 1993) were first converted to ADW by subtracting 10 %.

Table 8.5 Overview of the available data per functional unit and per spatial compartment in the Schelde estuary

Compartment	2	3	4	5	6	7	8	9	10	11	12	13
Zooplankton	•	•	•	•	•	•	•	•	•	•	•	•
Primary production	•		•	•	•	•		•	•	•	•	•
Macrobenthos					•	•	•		•	•	•	•
Hyperbenthos	•	•	•	•	•	•	•	•	•	•	•	•
Epibenthos & fish			•	•	•	•	•	•	•	•	•	•

8.3 Results and discussion

The results of the present data compilation and the biomass patterns reported by Hummel *et al.* (1988b) are shown in Fig. 8.11 through Fig. 8.15.

Besides proposing the two food chain hypothesis Hummel *et al.* (1988b) also split the tidal part of the river into three zones: a fresh water tidal zone from Gent to Antwerpen which falls outside the scope of the present study, a brackish tidal zone (Antwerpen to Hansweert) and a marine tidal zone (Hansweert to Vlissingen). This second division was confirmed in the community structure of the zooplankton (Soetaert & Van Rijswijk 1993), the macrobenthos (Meire *et al.* 1991), the hyperbenthos (Mees

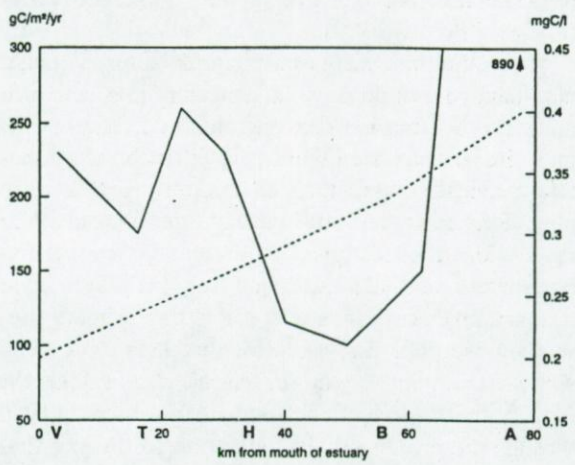

Fig. 8.11 Primary production (left axis, full line, van Spaendonk *et al.* 1993) and phytoplankton biomass (right axis, broken line, Hummel *et al.* 1988b) along the salinity gradient in the Schelde estuary. V = Vlissingen, T = Terneuzen, H = Hansweert, B = Bath, A = Antwerpen

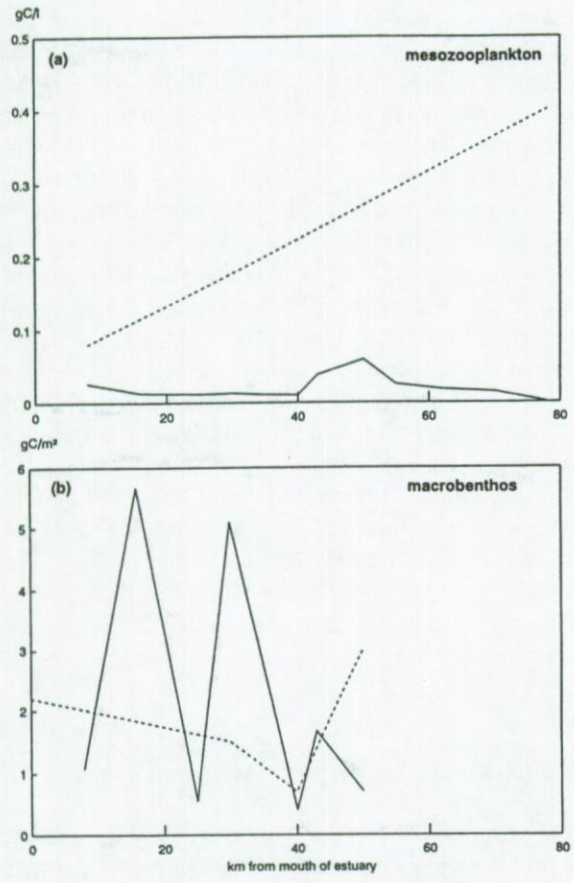

Fig. 8.12 Trends in biomass along the salinity gradient in the Schelde estuary: (a) mesozooplankton (full line, Soetaert & Van Rijswijk 1993; broken line, Hummel *et al.* 1988b); (b) macrobenthos, limited to the Westerschelde (full line, Craeymeersch *et al.* 1992; broken line, Hummel *et al.* 1988b)

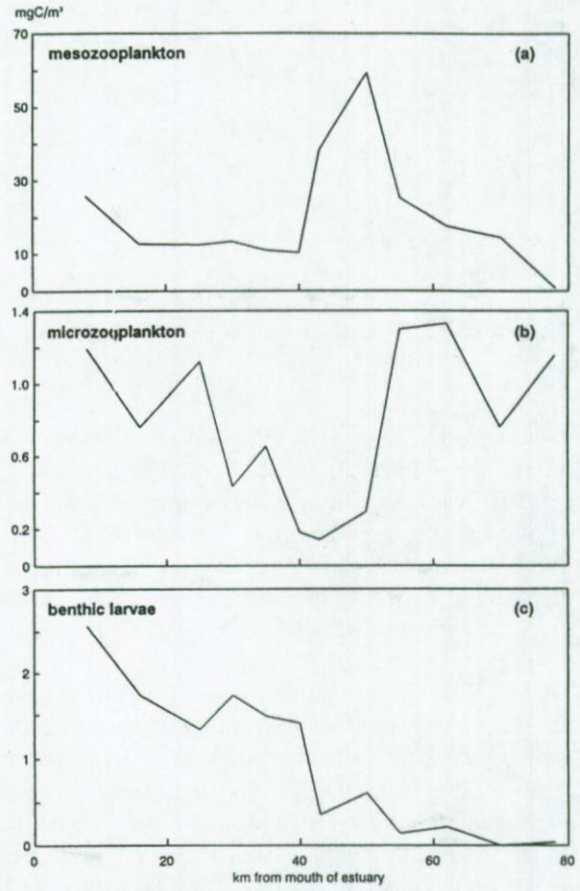

Fig. 8.13 Trends in biomass along the salinity gradient in the Schelde estuary: (a) mesozooplankton, (b) microzooplankton, (c) benthic larvae (Soetaert & Van Rijswijk 1993)

& Hamerlynck 1992, Mees *et al.* 1993b) and the epibenthic invertebrates and fishes (Chapter 2-Add.2) and therefore seems very robust.

Though it is difficult to compare chlorophyll a concentrations from Hummel *et al.* (1988b) with production figures given in van Spaendonk *et al.* (1993), these authors also provide peak concentrations of chlorophyll a at a few stations which broadly confirm the link between phytoplankton biomass, expressed as chlorophyll a concentrations and primary production. Peak concentrations in the marine part (Hansweert) are higher than in the brackish part (Bath), but the biomass peak in Antwerpen is 10 to 20 times higher than those peaks (van Spaendonk *et al.* 1993). In the Hummel model phytoplankton biomass was essentially increasing from the mouth up to Antwerpen even if they also stated that primary production was low in the turbid brackish zone (Fig. 8.11). According to van Spaendonk *et al.* (1993) the high primary production around Antwerpen in 1989 was mostly due to salinity intolerant freshwater species that would not survive transport to the turbid brackish zone. In the rest of the estuary primary production was found to be essentially light limited. However, as there may be a high variability in the patterns of chlorophyll a and primary production among years, more data are still required to come to more robust conclusions regarding this functional unit in the Westerschelde.

For the zooplankton (which in their definition corresponds to the mesozooplankton) Hummel *et al.* (1988b) also reported a gradual increase in biomass from Vlissingen to Antwerpen (and a steep decline further upstream). Besides the fact that the biomass reported by Hummel *et al.* (1988b) seems an order of magnitude too high (Fig. 8.12a) (they even reported more zooplankton than phytoplankton in the brackish part, possibly their zooplankton data refer to the spring bloom only?), a very clear bimodal pattern in mesozooplankton biomass could be found with the peak in the brackish part (predominantly *Eurytemora affinis*) about double (Fig. 8.13a) the peak at the mouth of the estuary (a mixture of coastal species). The mesozooplankton decreases rapidly east of Bath as a consequence of hypoxia. The peak in primary production and the peak in *Eurytemora affinis* are separated by about 30 km. In between (Fig. 8.13b) there is a clear peak in the microzooplankton - as quantified by Soetaert & Van Rijswijk (1993) -, which in this part of the system consists mostly of Rotifera, a group relatively resistant to hypoxia and an essential link for opening up the microbial loop

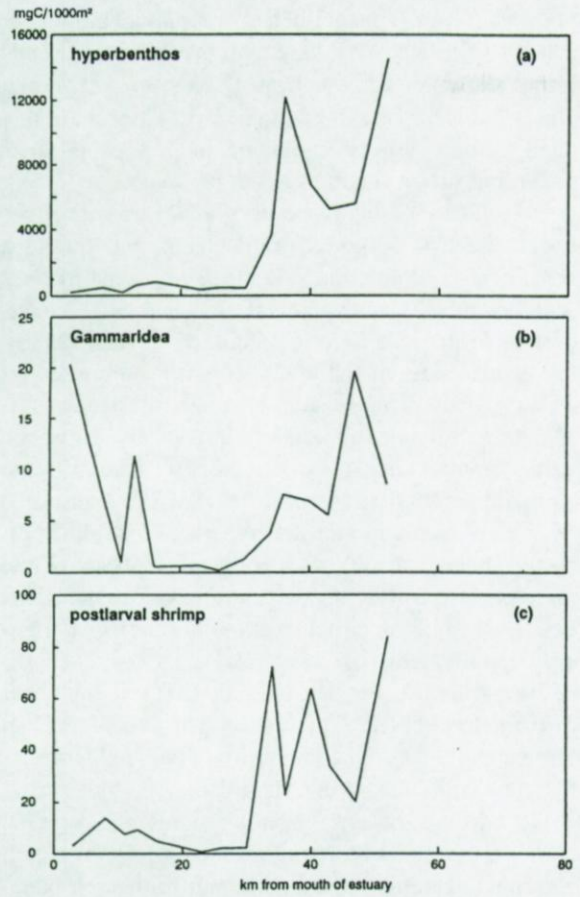

Fig. 8.14 Trends in biomass along the salinity gradient in the Westerschelde: (a) total hyperbenthos, (b) Gammaridea, (c) postlarval shrimp (Mees *et al.* 1993b)

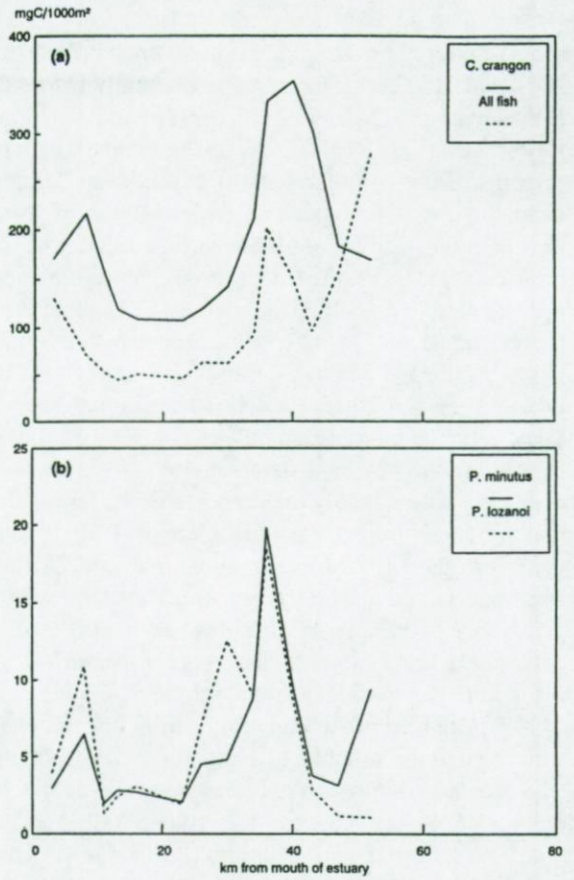

Fig. 8.15 Trends in biomass along the salinity gradient in the Westerschelde: (a) brown shrimp *Crangon crangon* (full line) and all demersal fish (broken line); (b) two gobiid species *Pomatoschistus minutus* (full line) and *P. lozanoi* (broken line) (Chapter 2-Add.2)

(Azam *et al.* 1983) for higher trophic levels. According to Fenchel (1988) the bacterial production is consumed by heterotrophic nanoflagellates and protozoans (all associated to the particulate detritus), which in turn are taken by ciliates, heterotrophic dinoflagellates and Rotifera.

A clear representative of the coastal food chain in the zooplankton are the meroplankton (planktonic larvae of benthic animals) which decrease gradually from the mouth to the brackish part (Fig. 8.13c).

A trend line through the macrobenthos biomass (Fig. 8.12b) would more or less conform to the bimodal pattern reported by Hummel *et al.* (1988b) except that the average biomass in the marine part reported in the present study is about four times higher than the biomass in the brackish part. Hummel *et al.* (1988b) reported a 1.5 times higher mean biomass in the brackish part than in the marine part. Even going back to the original data used by Hummel *et al.* (1988b) this higher peak in the brackish zone could not be retrieved. It is well documented that the macrobenthos in the brackish part is dominated by deposit-feeders dependent on sedimenting detritus for their food supply (Meire *et al.* 1991). In the marine part the suspension-feeders dominate and these depend mostly on primary production filtered from the water column (Herman & Scholten 1990). In spite of this, there does not seem to be a good correlation between primary production and macrobenthic biomass in the marine part. Though both rise steeply west of Hansweert there is a primary production peak spatially coinciding with a deep macrobenthic biomass trough at about 25 km from the mouth, east of Terneuzen. The variability in macrobenthic biomass in the marine part seems to be extremely high and would at first sight seem to make any conclusions about this functional unit impossible. However, suspension-feeders do not only need primary production, they also need relatively stable sediments and not too many indigestible particles in the water column. They therefore prefer areas with current velocities below 0.6 m s^{-1} (Dijkema 1988). Preliminary data from the 2D hydrodynamical model of the Westerschelde (Portelo *et al.* 1992) suggest the two peaks coincide with two compartment subareas (both at the outer curve of a relatively sharp turn in the main ebb channel) where current velocities are consistently lower than in other parts of the marine zone (R. Nevez, pers. comm.).

The hyperbenthos has only recently been discovered to be an important component of the Westerschelde ecosystem, both structurally (Mees & Hamerlynck 1992, Mees *et al.* 1993b) and functionally (Mees *et al.* 1994). Most of the biomass pattern shown in Fig. 8.14a consists of Mysidacea. Coming from the sea a first peak in hyperbenthos biomass occurs in the vicinity of Hansweert. A second, larger peak coincides with the trough in primary production and the copepod peak in the vicinity of Bath. It is at present unclear what may be the cause of the bimodality within the peak in the brackish part. Some of this may be smoothed out when true annual means, based on the monthly samples taken (Mees 1994) instead of the seasonal data reported here, become available. Alternatively the presence of the large tidal marsh of Saeftinghe or some aspect of the hydrodynamics in the brackish part may be involved. Within some species groups a clearly bimodal pattern, with a peak close to the mouth of the estuary and a second peak in the brackish part, can be observed, an example are the gammaridean amphipods (Fig. 8.14b).

Data on fish and epibenthic invertebrates were also not available to Hummel *et al.* (1988b). The brown shrimp *Crangon crangon* is the dominant epibenthic invertebrate in the system (Chapter 2-Add.2) and both the adult shrimp (Fig. 8.15a) and the hyperbenthic living juvenile postlarval shrimp of less than 20 mm total length (Fig. 8.14c) display a clearly bimodal pattern with a smaller peak close to the mouth of the estuary and a large peak in the brackish part. The biomass pattern of the demersal fish is rather similar to the pattern in the adult shrimp (Fig. 8.15a). The two-peaked structure within the brackish part is very similar to the observed pattern in the hyperbenthos (Fig. 8.14a). Possibly the fish fauna is entirely dependent on the hyperbenthos in this part of the system. Within the fish the dominant components are flatfish and gobies (Chapter 2-Add.2). Within the gobies the bimodal pattern is clear, both in *Pomatoschistus minutus* and *Pomatoschistus lozanoi* (Fig. 8.15b).

At present there are insufficient data on piscivorous birds to extend the analysis to that unit (Stuart *et al.* 1990). Also, though anecdotal observations suggest seals are predominantly recorded around the Hooge Platen close to the mouth and on the Plaat van Valkenisse in the brackish part, as for the birds, coverage in the middle part of the estuary is too low to allow any firm conclusions to be drawn at present.

The results of the present study suggest that there are indeed two separate food chains in the Westerschelde as suggested by Hummel *et al.* (1988b) and that a bimodal pattern of biomass distribution along the estuarine gradient is present, at least in the pelagic functional units. This pattern propagates through to the higher trophic levels. It is unclear how Hummel *et al.* (1988b) arrived at their hypothesis from the data they had compiled. Hummel *et al.* 1988b) stated that most of the biomass trends found show an increase from the sea to Antwerpen and that this may seem contradictory. They claim this contradiction will be explained in § 3.3.1 of their paper, but such a section can not be found.

There seems to be no gradual transition between the two purported food chains and they are separated by an intermediate "desertic" zone of over 20 km width. As an explanatory mechanism it is suggested, in accordance with Hummel *et al.* (1988b), that the richness of the brackish part is supported by a detritus based food chain. Virtually all of the non-refractory organic material in this zone would be either re-mineralised by the intense heterotrophic bacterial activity (Goosen *et al.* 1992) or consumed by the zooplankton and the hyperbenthos, either directly or through the microzooplankton. Part of the material also settles on the bottom and sustains the deposit-feeding macrofauna. Possibly part of the energy requirements of shrimp are also sustained directly by detritus (or detritus plus bacteria and other micro-heterotrophs). This "second trophic level" in turn supports the rich community of epibenthic invertebrates (crabs and shrimp) and fish.

In the "desertic" zone the remaining organic matter is presumably mainly refractory. There is still a surplus of nutrients available and primary production is relatively high. Possibly as a consequence of high current velocities this primary production cannot be used very efficiently by the macrobenthos, except in a few relatively low turbulence sites where the suspension-feeders thrive. Still, it remains unclear why the zooplankton is not capable of exploiting the primary production in this zone.

Towards the mouth of the estuary primary production remains high and a coastal food chain flourishes. At the second trophic level species composition differs substantially in some groups, *e.g* the zooplankton (Soetaert & Van Rijswijk 1993) and the hyperbenthos (Mees *et al.* 1993a). At the next trophic level the dominant species in both food chains are rather similar. That the observed bimodal pattern is caused by the underlying food chains and not by the physiologic limits of the respective organisms can be seen from the distribution in shrimp and gobies where the bimodal pattern can be observed within single species. Secondary support for the subordinate (if any) role of physiological limitation is provided by the fact that *Neomysis integer* has its peak distribution at much higher salinities in the Westerschelde than in the other European estuaries (Mees *et al.* 1995). Fecundity and growth in the Westerschelde are comparable or higher than those recorded in the other areas (Mees *et al.* 1995) indicating that the animals are not particularly stressed.

The role of the tidal marshes within the brackish part is less clear at present. At high tide they are intensively used by both hyperbenthic crusta-

ceans (Cattrijsse *et al.* 1993, Mees *et al.* 1993a) and juvenile stages of fishes (Cattrijsse *et al.* 1994, Frid & James 1988) and may thus form an integral part of the food web of the estuary. Logically, as tidal marshes are sinks for mud they should be net importers and not net exporters of organic matter. This high input of organic matter may be one of the attractants for the mobile fauna. Presumably added to that there is a substantial primary production by the diatom phytobenthos in the sheltered tidal creeks. It is also possible that there may be a qualitative edge to foraging in a tidal marsh related to the characteristic lipid quality reported for a nearby coastal marsh by Hemminga *et al.* (1992). Several mysid species, both coastal zone species and estuarine endemics, move into the tidal marshes to release their larvae (Mees *et al.* 1993a). In view of the high densities of fish and shrimp in the marsh (Cattrijsse 1994), instead of being a strategy of predator avoidance, this behaviour may also be related to food quality.

The obvious next step for a better understanding of the system and especially of its characteristic heterotrophic food chain in the brackish part is the detailed investigation of the link between the bacterial production and the higher trophic levels. Are it really the detritus-associated bacteria that form the basis of the food chain and are they consumed as such by the next links, *i.e.* the mesozooplankton and the mysids? It seems unlikely that copepods and mysids, in view of their short and uncomplicated digestive systems are able to incorporate unmodified plant detrital material with its characteristic C/N ratio to a great extent. However, it is also known that mysids possess cellulases (Mann 1988) so the alternative hypothesis, namely that bacteria and metazoa compete for the same detritus can as yet not be ruled out. The polluted Westerschelde (see Chapter 1) may be a particularly interesting system for the analysis of the energy transfers under consideration here because some of the important functional units are spatially segregated due to the gradient in dissolved oxygen (and not as a result of transport processes because of the high residence time of the water). This should facilitate the analysis of the underlying processes.

8.4 Conclusions

Except for the bimodality in the macrobenthos biomass reported by Hummel *et al.* (1988b) none of the patterns in their other functional units were suggestive of the existence of two separate food chains. They have therefore probably proposed their model intuitively. As is often the case they were right but for the wrong reasons.

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CHAPTER 9 THE DEMERSAL FISH AND MACRO-INVERTEBRATE ASSEMBLAGES OF THE WESTERSCHELDE AND OOSTERSCHELDE ESTUARIES: OVERVIEW AND FINAL CONCLUSIONS

K. Hostens

Abstract. *An overview on the nursery function of the Westerschelde and the Oosterschelde estuaries for demersal fish and macro-invertebrates is presented, based on all data sets presented in this thesis. The present thesis provides a baseline, and suggests that both the Westerschelde and Oosterschelde estuaries play a significant role as nursery areas for several demersal fish and macro-invertebrate species. The forcing factors for recruitment and the seasonal appearance of (post)larval fish and macro-crustaceans are explained. Biodiversity is related to habitat use and habitat availability. The faunas of the Westerschelde and Oosterschelde are structured by a limited number of environmental variables, and the prediction of species occurrence by means of single-species logistic models is discussed. Spatial, long-term and seasonal patterns in density in relation to the environment are summarized by means of multivariate analyses and graphical representation of trends per species and per taxonomic group. The seasonal appearance of both (post)larval and juvenile fish and macro-crustaceans in the Westerschelde is described. Density of the commonest species is predicted by means of single-species linear regression models. A short description of the human impact on the fish and macro-invertebrate assemblages is given. In the functional part of this overview, a generalized food web for the Westerschelde is presented, and the importance of mysids as prey for several fish and macro-crustaceans in the Westerschelde is discussed. Finally, 10 major conclusions and some remarks are formulated and some recommendations for future research are given.*

9.1 Introduction

The thesis focuses on the nursery function of the Westerschelde and Oosterschelde estuaries for demersal fish and macro-invertebrate species. Long-term monitoring in a more or less uniform way has produced a large amount of data on the ecology of the demersal fish and macro-invertebrate fauna in the Dutch Delta area (SW Netherlands), and in the Westerschelde and Oosterschelde estuary in particular. The huge data sets used in the present thesis cover two decades from 1983 through 2001, although a large gap exists from 1993 till 1998 (see Chapter 1).

The bulk of the thesis is based on the 3-m beam trawl surveys in the subtidal, where a total of 2100 samples were taken during diurnal, fortnightly, monthly and/or quarterly surveys (see Table 1.2). From these, 36 % were gathered in the Westerschelde in the period 1988-1992, and 51 % in the Oosterschelde in the period 1983-1989. Only 5 and 8 % of the subtidal samples were gathered in the period 1999-2001 in the Westerschelde and Oosterschelde, respectively. Data from the ebb-tidal deltas of the Oosterschelde and the Grevelingen (part of the Voordelta, 617 samples) were mainly used in the addenda to several chapters. Data on juvenile fish and macro-invertebrates from the intertidal covered a limited time span, and were only partly used. In the brackish part of the Westerschelde, 139 intertidal samples were gathered in 1992 with a 2-m beam trawl. In the Oosterschelde, the 2-m beam trawl samples (period 1984-'85) were not used; data from 860 fyke samples (period 1979-'88) were used in an addendum. See Fig. 9.1 for a map of the study area. Throughout this synthesis, several paragraphs are based on only part of the data, either for a better representation of the underlying patterns or for comparative reasons.

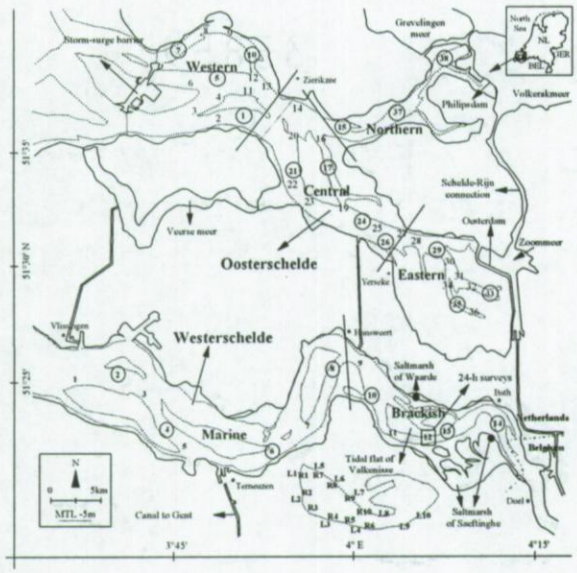


Fig. 9.1 Map of the Westerschelde and Oosterschelde estuary, indicating the sampling locations in the different subhabitats, and the division in different zones

The nursery function of an estuary depends on recruitment of (post)larvae into the system, habitat complexity and availability, environmental properties (hydrographic regime), and prey availability. The environmental/biological and biological/biological interactions act both as extrinsic and intrinsic forcing variables on the structure of the demersal fish and macro-invertebrate assemblages (see Chapter 1). The thesis benefits from the complementary research on other ecosystem components in both estuaries. In this overview, the seasonal appearance or recruitment of (post)larval fish and crustaceans in the hyperbenthal of both estuaries and in the intertidal saltmarsh creeks of the Westerschelde is summarized, and related to the seasonal and spatial distribution patterns of the juvenile fish and (adult) macro-invertebrates in the subtidal and brackish intertidal of the Westerschelde.

The relation between a limited set of environmental variables and the structural patterns in diversity, density, biomass (and growth) of the juvenile fish and macro-invertebrate fauna, either at community or at species level, forms a major component of the present thesis (PART I, Chapters 2 to 6). Both spatial and seasonal patterns at several scales, *i.e.* between and within estuaries and subhabitats, and short-, mid- and long-term changes, are investigated. The results of different graphical and statistical approaches are summarized. In PART II of the thesis (Chapters 7 and 8), the functional patterns in diet and feeding behavior of several fish and macrocrustaceans in the Westerschelde are investigated. The importance of hyperbenthic organisms – and mysids in particular – in the food web of the Westerschelde is emphasized.

Fish and macro-invertebrates are considered to be good biological indicators, although it may be difficult to differentiate between human induced and natural changes in the communities. The human impact on the structure and functioning of demersal fish and macro-invertebrate assemblages is briefly touched upon in this overview.

9.2 Recruitment

The term recruitment is often been used ambiguously. Fishery biologists are mainly interested in the 'recruitment' of juveniles to the adult exploitable stock (Beverton & Holt 1957). Here, it is preferred to refer to this type of recruitment as 'juvenile production', and to use the term 'recruitment' for larval transport towards and retention within the nursery areas.

9.2.1 Forcing factors

The nursery function of an estuary depends on the supply of (post)larvae to the system, which in turn depends upon (1) the reproductive success of the adults, (2) the distance from the spawning areas, (3) larval survival, (4) efficiency of larval transport, and (5) efficiency of larval retention (Potter *et al.* 1997).

Most of these parameters depend on forcing factors outside the estuary. The reproductive success, for example, is dependent on population viability, genetic structure, size and maturity of the breeding population, and fecundity. These factors themselves may be influenced by overfishing (through resource removal), environmental pollution, geomorphological and hydrographical changes (Daan *et al.* 1990).

For a number of commercial species, the spawning grounds are relatively well-known, *e.g.* plaice *Pleuronectes platessa* spawns in four major areas in the North Sea, mainly in the Southern Bight (Simpson 1959). Several flatfish and gadoid species spawn close to the nursery areas. Still, after more than a century of intensive investigations, the knowledge on the basic breeding biology of most commercial and non-commercial species remains patchy (Daan *et al.* 1990). The majority of marine spawners (including all commercial gadoids, flatfish and several clupeoids) produce large numbers of small pelagic eggs, which are quickly hatched (Costa *et al.* 2002). This is the case for 50 % of the species in the Westerschelde (Cattrijsse & Hampel 2000). Only few species (*e.g.* gobies) spawn or may be able to spawn (large, demersal eggs) in the estuary proper.

Larval survival depends on a whole range of abiotic and biotic parameters. A thorough discussion is given in Costa *et al.* (2002).

Although transport and retention efficiency may be difficult to estimate, it has been shown that larvae of several species are passively transported by means of appropriate currents towards the nurseries

Table 9.1 Seasonal appearance and number of (post)larval fish and macro-crustacean species, with the number of species present with 2 life history stages between brackets

Season	Subtidal Westerschelde		Subtidal Oosterschelde		Intertidal Saeftinghe saltmarsh creek		All areas	
	macro-crust.	fish	macro-crust.	fish	macro-crust.	fish	macro-crust.	fish
Winter	-	1	-	2	-	-	-	3
Winter-Spring	-	3	-	-	-	3	-	4
Spring	6 (4)	6	4 (2)	6	-	4	4 (1)	10
Spring-Summer	2	-	2 (1)	-	2 (1)	1	3 (2)	1
Summer	2	2	3 (1)	-	4 (2)	3	5 (1)	4
Autumn	-	-	1	-	-	-	1	-
Total	**9 (5)**	**11**	**8 (6)**	**8**	**5 (2)**	**9**	**11 (6)**	**17**

(larval drift) (Miller *et al.* 1988), and/or actively migrate into and within the nursery areas (selective tidal stream transport) (De Veen 1978, Hedvall *et al.* 1998, Jager 1999). In the North Frisian Wadden Sea, (post)larvae of several flatfish species and of brown shrimp *Crangon crangon* are retained in puddles on the tidal flats during low tide (Berghahn 1983). No such data exist for the Delta area, but we know that (post)larvae of 11 macro-crustaceans (of which 6 species with 2 different life stages) and 17 fish species do enter the Westerschelde and/or Oosterschelde estuary (Table 9.1) The diversity will even be higher, as the postlarvae of the different gobiid and clupeoid species were not (or could not be) identified to species level in the different habitats (see also Beyst *et al.* 1999). The (post)larval data presented here, were taken from Mees (1994) and Cattrijsse (1994) for the period August 1990 – May 1991, and from Chavatte (2001) and Hampel *et al.* (in press) for the period August 1999-May 2000.

9.2.2 Seasonal appearance

Larval and early postlarval fish and macro-crustaceans, constitute the major part of the mero-hyperbenthos, and only appear for a short period, mainly in spring, in the Westerschelde and Oosterschelde estuaries, although several species extend their larval appearance either towards late winter or early summer. A summary on the presence of (post)larval fishes in the Westerschelde and the Voordelta for the period 1988-'91 was given in Beyst *et al.* (1999).

Seasonal appearance may be an important regulating factor, as several species undergo metamorphosis in the nursery areas, and changes in the diet have to match prey availability (Costa *et al.* 2002).

9.2.3 (Post)larval macro-crustaceans

The number of (post)larval macro-crustacean species was lowest intertidally. Highest abundances (maximum 40 ind m^{-3} in June 1990) of postlarval *C. crangon* were recorded in the intertidal saltmarsh creeks (on average 1 to 2 orders of magnitude higher than in the subtidal) (Fig. 9.2a). Zoea larvae of *C. crangon* are rapidly transported from the sea towards these intertidal saltmarsh creeks 50 km upstream in the brackish part of the Westerschelde. This can only be achieved through active and selective tidal transport. In the mean time the larvae undergo metamorphosis to the postlarval stage, as no zoeae were recorded from the marsh creeks. The nursery function of these creeks as refuges and foraging areas for the brown shrimp has been discussed in Cattrijsse *et al.* (1997). Three other caridean (prawn) species were only sporadically caught.

Other important macro-crustaceans were zoea and megalopa larvae of both brachyuran and anomuran crabs. In the intertidal marsh creeks only shore crab (*Carcinus maenas*) larvae were present. Higher densities of *C. maenas*, but also of flying crab *Liocarcinus holsatus*, spider crabs *Macropodia* and both anomuran crabs *Pagurus bernhardus* and *Pisidia longicornis*, were noted in the subtidal Oosterschelde. This is probably related to the habitat complexity and vegetation structure. In a nursery along the Swedish west coast, *C. maenas* megalopae actively selected habitats with filamentous algae, which provide the best refuge from predation (Hedvall *et al.* 1998).

Note the absence in 1999-2000 of all macro-crustacean (post)larvae from the brackish subtidal Westerschelde, of shrimp postlarvae from the north-

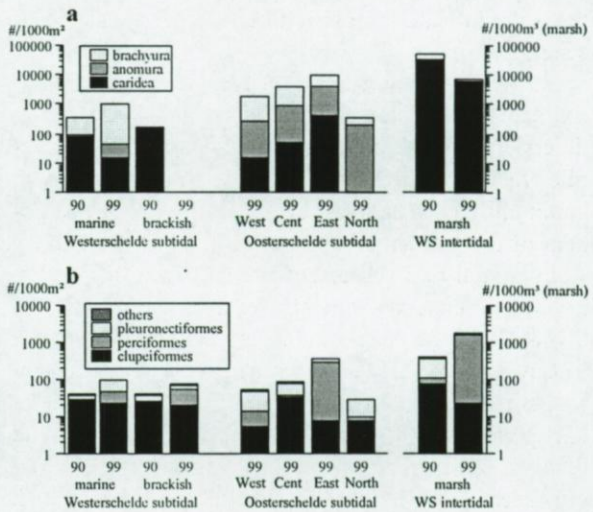


Fig. 9.2 Spatial and long-term patterns in (a) (post)larval macro-invertebrates and (b) fish groups, based on the maximum densities (log-scale) in the subtidal (ind 1000 m^{-2}) Westerschelde and Oosterschelde, and in an intertidal creek (ind 1000 m^{-3}) in the saltmarsh of Saeftinghe, for the periods 1990-'91 and 1999-2000

ern subtidal Oosterschelde, and of brachyuran larvae from the intertidal saltmarsh. Probably, the short peak abundance was missed due to the quarterly survey design.

9.2.4 (Post)larval fish

The (post)larval fish diversity was comparable in all subhabitats (Table 9.1). Of the 17 postlarval fish species, only 4 (probably 7) species were common in all subhabitats (Fig. 9.2b): clupeoids (sprat *Sprattus sprattus* and herring *Clupea harengus*), gobies (probably 3 species of the genus *Pomatoschistus* in different subhabitats), and flatfish (sole *Solea solea* and flounder *Platichthys flesus* (the latter not in the Oosterschelde). The other postlarval fish species (6 percids, 2 gadoids, 1 flatfish and 4 others) were only sporadically recorded.

The intertidal creeks also harbored higher densities of postlarval fish, mainly high densities of common goby *Pomatoschistus microps* and seabass *Dicentrarchus labrax* in spring-summer 1999, and flounder *Platichthys flesus* in spring of both periods. Clupeoids were equally abundant in the different subtidal parts of the Westerschelde and Oosterschelde, while gobies were mainly present in the brackish Westerschelde and in the eastern part of the Oosterschelde. A discussion on the presence of the fish larvae in the Dutch Delta area was presented by Beyst *et al.* (1999).

9.3 Biodiversity

9.3.1 Habitat availability

The biodiversity of fish (and macro-invertebrate) species within an area is a function of habitat diversity, niche availability and area size (Wootton 1992). The reader is referred to Pihl *et al.* (2002) for a thorough discussion on habitat types, habitat extent and habitat use, including the references for the Westerschelde and Oosterschelde (although the values are different, as more data were available for the present study).

Of the nine distinguished estuarine habitat types, subtidal and intertidal soft substratum make up >75 % of the total habitat in both estuaries (Fig. 9.3a & b). This was comparable with other European estuaries in the Boreal/Atlantic region (Pihl *et al.* 2002). The intertidal saltmarsh area in the Westerschelde is largely allocated to the brackish saltmarsh of Saeftinghe, while in the Oosterschelde most saltmarshes disappeared after the major engineering works.

As the data for this paragraph were based on the whole estuarine environment, tidal freshwater and reedbeds were included as habitats, but these are only found in the Zeeschelde, *i.e.* the upstream part of the Schelde estuary (see Chapter 1).

In the Oosterschelde, the intertidal and subtidal habitats are further extended with the presence of biogenic reefs (mainly mussels and oysters) and hard substratum.

9.3.2 Overall fish diversity

Based on all data gathered by different institutes during the last two decades in both estuaries, the total number of fish species amounted to 96, of which 74 species were recorded in the Schelde and 75 species in the Oosterschelde. These values include 15 and 3 additional species to the data given in Pihl *et al.* (2002) for the Schelde and Oosterschelde, respec-

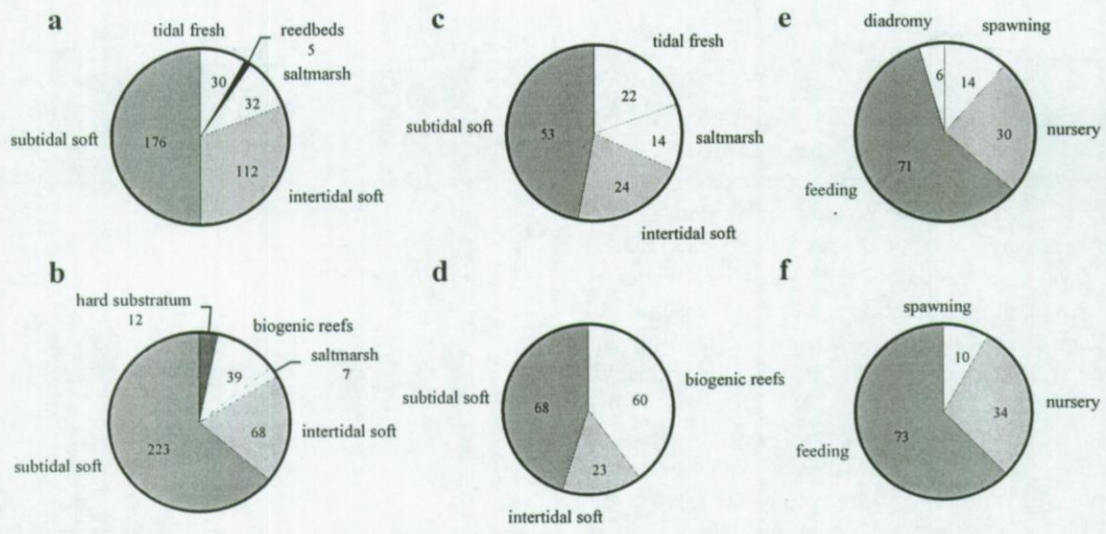


Fig. 9.3 Relative presence of the different habitat types, with the area surface given in km² (a,b), fish diversity in the different habitats (c,d), and number of fish species per habitat use, based on all available data from literature from the last two decades in the Schelde (upper pie charts) and the Oosterschelde (lower pie charts)

tively. This indicates that species richness depends on the extent of the study period and area size (Elliott & Dewailly 1995). However, the total number of species is comparable to that of several estuaries in the NW Atlantic/Boreal region (*e.g.* the Weser/Elbe, Humber, Seine and Tagus estuaries).

Most of the species were recorded in the subtidal hatitats (although no data exist for presence on the hard substratum), while only a limited number of species were recorded in the intertidal (the value for the Oosterschelde given in Pihl *et al.* (2002) is incorrect) (Fig. 9.3c & d). Surprisingly, 22 fish species were recorded from the tidal freshwater part of the Schelde estuary during the 1990s, related to an improved water quality in the upstream part.

9.3.3 Habitat use

In respect to habitat use, 14 (10) species normally should be able to spawn in the estuary proper (Fig. 9.3e & f). However, for most species we believe no spawning activity takes place. Fish eggs (mainly from *Solea solea* and *Pomatoschistus* species) were recorded in the hyperbenthic sledge samples from both estuaries and in the ebb-tidal deltas (Beyst *et al.* 1999). Yet, it cannot be claimed that these originated from local spawning activities (Cattrijsse & Hampel 2000).

Only six diadromous species were recorded in the Westerschelde and none in the Oosterschelde. The physical constructions (*e.g.* barrages and dams), the absence of suitable habitats at the riverine side, and the relatively bad water quality conditions in the Zeeschelde during most part of the year are the main reasons for the low representation of this ecological guild. The same holds for most European estuaries (Pihl *et al.* 2002).

Most of the marine adventitious, freshwater and marine juvenile species (Elliott & Dewailly 1995) enter the estuary for feeding purposes. Juveniles of *ca.* 30 marine and estuarine resident species use the Westerschelde and Oosterschelde as nursery areas. These are of main interest in the present thesis and in the rest of this chapter.

9.3.4 Juvenile fish and macro-invertebrate diversity

The following paragraph is based on quarterly subtidal data from both estuaries for the periods February 1988 – November 1989 and Februay 2000 - November 2001. As the sampling period is much shorter, the number of juvenile fish and macro-invertebrate species is much lower as well, with a total of 32 fish and 6 macro-invertebrate species in the Westerschelde, and 41 fish and 31 macro-invertebrate species in the Oosterschelde (see Chapter 3, Chapter 2, Chapter 5). In comparison, 40 species were listed for the Schelde in the period before the 1940s (Poll 1945, Van Damme *et al.* 1994), and 44 fish species were recorded in the period 1960-'76 in the former open Oosterschelde estuary (Doornbos *et al.* 1981).

On average 16 fish and only 3 macro-crustacean species were recorded per season in both the marine and brackish parts of the Westerschelde, with a little higher values in spring (Fig. 9.4a-c). The low number of macro-invertebrates (3 brachyuran crabs, 2 caridean prawns and 1 caridean shrimp) is mainly attributed to the fact that only few species can withstand the harsh estuarine conditions, *e.g.* rather low and largely fluctuating salinities and much higher turbidities (Chapter 5).

In the Oosterschelde the fish diversity was higher in 2000-2001 compared to 1988-89, with on

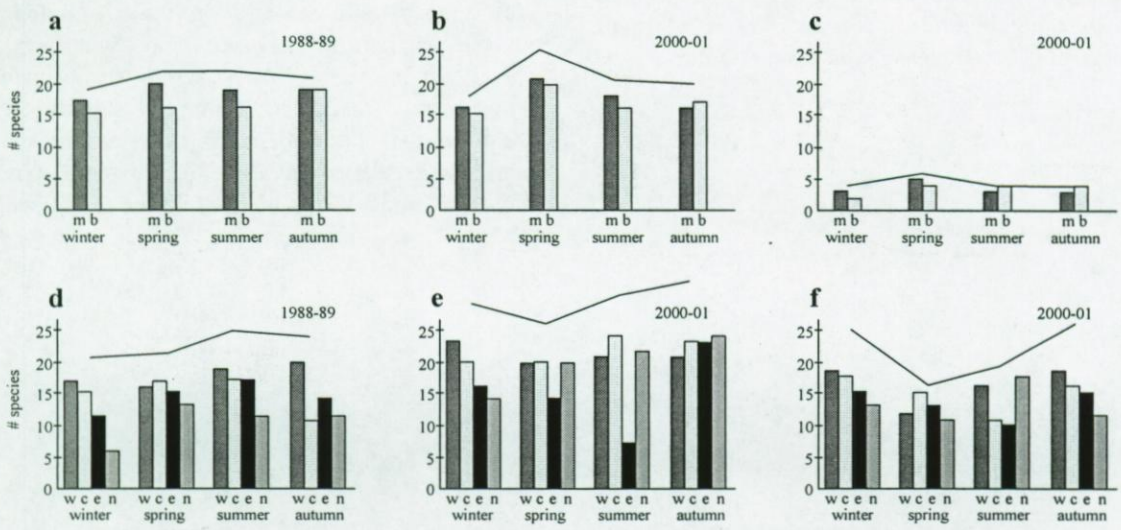


Fig. 9.4 Fish (a-b, d-e) and macro-invertebrate (c,f) diversity in the Westerschelde (a-c) and Oosterschelde (d-f) for the periods 1988-'89 and 2000-2001, per season and per subhabitat: marine (m) and brackish (b) parts in the Westerschelde, western (w), central (c), eastern (e) and northern (n) parts in the Oosterschelde

average 7 to 24 species per season (Fig. 9.4d & e). The macro-invertebrate diversity was much higher throughout the Oosterschelde compared to the Westerschelde, with a minimum of 16 species in spring (Fig. 9.4f). The large habitat complexity in the Oosterschelde (soft-hard substrate, mussel beds, macro-algae) seems to favour the occurrence of the macro-invertebrate fauna, constituted of 10 brachyuran crabs, 9 caridean prawns, 5 (6) echinoderms, 3 caridean shrimps, 3 cephalopods and 2 anomuran crabs (Chapter 5).

The juvenile fish species present in the Westerschelde and Oosterschelde (the second values between brackets) belonged to the clupeoids (4, 3), gadoids (3, 4), flatfish (8, 6), gobiids (4, 6), other percids (7, 8), scorpaenids (3, 4), pipefish (1, 3), and several other groups like salmonids, eels, atherinids and sticklebacks (2, 7). Several demersal fish species are eurytopic with a high tolerance towards a broad range of environmental conditions. Still, only few fish and macro-invertebrate species are really common in both estuaries. For example, only 3 fish and 7 macro-invertebrate species occurred in >70 % of the Oosterschelde samples (Chapter 4, Chapter 5). Moreover, in both systems, diversity was only a little higher in the more marine parts, showing a dominance of the seasonal pattern over the spatial pattern.

Diversity (surely of the macro-invertebrates) is influenced by the invasion of so-called alien species, mainly imported by means of anthropogenic transportations (Little 2000). In the Westerschelde, Chinese mitten crab *Eriocheir sinensis* was already imported during the beginning of 20th century. In the lower Zeeschelde, 3 of the 4 recorded crab species were 'exotics' (Maes *et al.* 1998a). In the Oosterschelde, arch-fronted swimming crab *Liocarcinus arcuatus* became the commonest swimming crab since it entered the system in 1982. Common species like *Carcinus maenas* and harbour crab *Liocarcinus depurator* might suffer the aggressive invasion of Japanese brush crab *Hemigrapsus penicillatus*, as has been shown in the Gulf of Biscay (d'Udekem d'Acoz 1999).

All these data prove that the diversity of the fish and macro-invertebrate assemblage is highly correlated with the occasional immigration of a large number of typical marine species at different times of the year. In conclusion, the main environmental variables influencing the biodiversity patterns were salinity/turbidity, sediment/habitat type and temperature.

9.4 Environmental properties

In temperate areas, the estuarine abiotic environment can be largely characterized by the patterns in salinity, temperature, turbidity, dissolved oxygen concentration, and sediment type. As such, these environmental variables and their combined effects are most likely to be the important controlling factors in the distribution of fish and macro-invertebrate assemblages (Elliott & Hemingway 2002). Patterns in current velocity and degree of exposure might be important characteristics of an estuary, but could not be measured at the sampling locations. The underlying patterns can partly be deduced from the sediment and turbidity characteristics. Several biological factors may be important as well.

The following paragraphs are based on quarterly data from the period 2000-2001, and give a general view of the spatial and seasonal patterns in temperature (°C), salinity (psu), dissolved oxygen concentration (mg l^{-1}) and turbidity (m^{-1}, measured as the reciprocal of secchi depth) in the Westerschelde and Oosterschelde estuaries.

Both on a spatial and seasonal scale, temperature more or less showed an inverse relationship with dissolved oxygen concentration in the Westerschelde, while salinity showed an inverse relationship with turbidity (Fig. 9.5 and Fig. 9.6). A comparable inverse relationship between temperature and dissolved oxygen in the Oosterschelde was only found on a seasonal scale. The figures for salinity clearly show that the Westerschelde is a true estuary, with a marked salinity gradient along the horizontal axis and higher salinities in summer, while the Oosterschelde

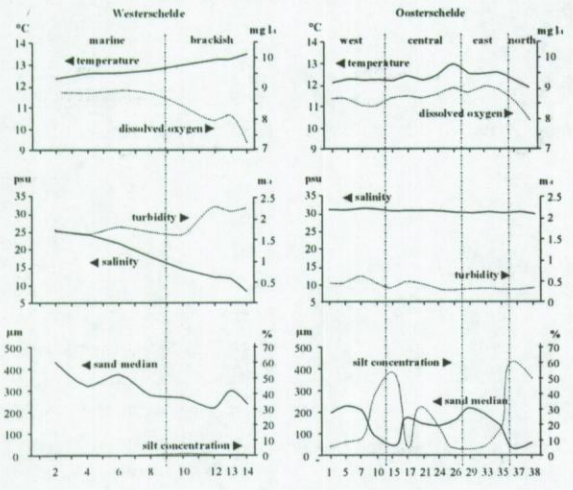


Fig. 9.5 Spatial patterns in six environmental variables in the Westerschelde and Oosterschelde estuaries

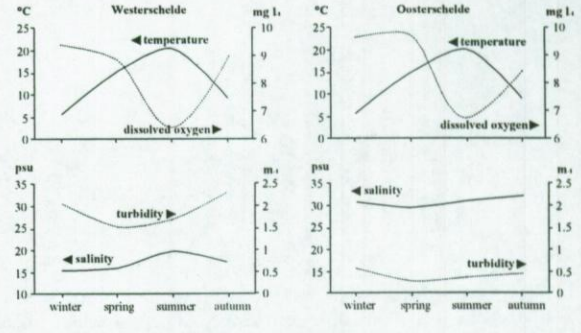


Fig. 9.6 Seasonal patterns in four environmental variables in the Westerschelde and Oosterschelde estuaries

is a marine bay with constant high salinities and low turbidities (5 times lower than in the Westerschelde) in all subareas throughout the year. The higher turbidities (and lower salinities) in the Westerschelde during the colder months are mainly due to higher river runoff (Heip 1989b).

A striking feature was the serious drop in dissolved oxygen concentration in the brackish part of the Westerschelde. The organic enrichment in this area, and the bacterial/microbial respiration related with the decaying processes (Heip *et al.* 1995) are the main reasons for this gradient. Also, the increased turbidity in the brackish part is related with the increased concentration of suspended matter in the water column, as sediment particles are retained for several days within the brackish part of the Westerschelde (Soetaert & Herman 1995b). The observed patterns were comparable with those found for the period 1988-'89 (Chapter 2). Also, in the northern part of the Oosterschelde, dissolved oxygen concentrations were lower, probably related with the currents and the high concentrations of mud in the sediment of this subarea. For most stations in the Oosterschelde the median grain size was below 250 µm, while in the Westerschelde the sand was coarser and gradually decreased from the marine to the brackish part.

9.5 Prediction of occurrence

Alterations in the environmental conditions can lead to changes in the estuarine populations of fish and macro-crustaceans (Chapter 6). A simultaneous examination of several different variables is often required to study ecosystem responses to perturbations (Jassby & Powell 1990). Still, for a sound ecological management, it might by useful to be able to predict the occurrence and distribution of fish and macrocrustacean species in the estuary.

We tried to predict the response of the 15 most common species (12 fish and 3 macroinvertebrate species) to (natural) changes in the environment in the Westerschelde. The probability of occurrence was modelled by means of single and multiple logistic regressions as quadratic functions of only 4 environmental variables (Chapter 6).

9.5.1 Single species response curves

Single species response curves yielded good descriptions of the occurrence of every species along the four environmental gradients (temperature, salinity, turbidity and dissolved oxygen concentration), which was related to the maximum likelihood of presence in the field (Chapter 6).

Several species responded the same way to the four environmental variables, if compared per ecological guild. For example, several marine juveniles were more likely to be found at higher salinities and lower turbidities (*e.g.* flying crab *Liocarcinus holsatus*) or at higher temperatures (*e.g.* sole *Solea solea*), while the opposite holds for a number of estuarine resident species (*e.g.* common goby *Pomatoschistus microps*).

Salinity is regarded as an extremely important variable for many animals and plants (Attrill *et al.* 1999). This is mainly related to the process of osmoregulation (Little 2000). The presence of several fish and macro-invertebrate species is limited exactly by salinity, and euryhalinity is a precondition for estuarine visitors and inhabitants (Blaber 1997). However, it is unlikely that those euryhaline species will be distributed over the full salinity regime they can tolerate (the potential niche), but rather will be limited to a kind of 'realized' niche (Little 2000). Also, with respect to the other environmental variables, it has been shown that most species are likely to be found within a limited range in the Westerschelde, which does not necessarily mean they are physically limited to these ranges.

In the Thames estuary (UK) it was shown that the combined effect of low salinity and low oxygen levels formed a barrier to migrating brown shrimp *Crangon crangon* (Jones & Wolff 1981). However, fish and macro-invertebrates are highly mobile, and can easily avoid unfavorable conditions. (*e.g.* low oxygen concentrations and high turbidity). On the other hand, turbidity may also be important in lowering predation pressure (Blaber & Blaber 1980).

9.5.2 Presence/Absence models

Changes in one variable (*e.g.* salinity) are usually accompanied by changes in several other parameters (*e.g.* current flow, oxygen levels, food supply and so on), which makes it difficult to decide if only one or several factors are important (Little 2000). It is argued that the combined interaction between different environmental variables will be more powerful to predict species occurrence (and density), than the single variables. In the following paragraph best-fitting models were built for the same 15 species, by means of multiple forward stepwise logistic regressions to predict presence/absence.

All response surfaces were highly significant when combining data on temperature, salinity, turbidity, dissolved oxygen concentration and/or their quadratic effects. The addition of other variables, such as current velocity, mysid prey density, chlorophyll a or suspended particulate matter, did not substantially improve the predictions. For most species the prediction of presence/absence was relatively successful, as 60-90 % of the occurrences were correctly predicted (Fig. 9.7). For the eight most common species, sensitivity (% present predicted as pre-

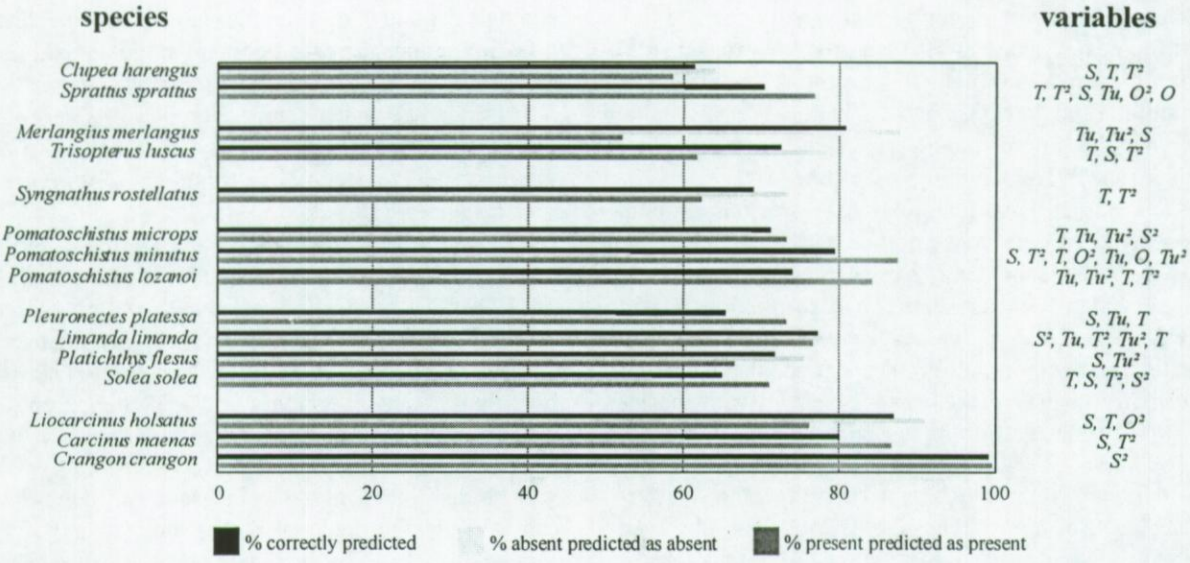


Fig. 9.7 Predictive success (% correct), specificity (% absent predicted as absent) and sensitivity (% present predicted as present) for the 15 presence/absence models, and the selected environmental variables (and/or the quadratic effects) in order of importance per model: temperature (T, T^2), salinity (S, S^2), dissolved oxygen concentration (O, O^2), and turbidity (Tu, Tu^2)

sent) was higher than specificity (% absent predicted as absent).

The presence of several fish and macro-crustaceans in the estuary is likely to be triggered by temperature. However, the presence/absence models showed that different environmental variables interact at both temporal and spatial scales. For example, the models for plaice *Pleuronectes platessa* and sand goby *Pomatoschistus minutus* predicted a higher probability of occurrence at lower temperatures (negative sign of the regression coefficient) and higher salinities (positive sign) (Chapter 6). This seemed contradictory to the fact that both species were more common in the 'brackish' part of the Westerschelde. Still, the predictions were in general agreement with the actual presence of plaice and sand goby, as both species were more common during the colder months in this part of the estuary, when the saltwedge penetrates deep into the middle reaches of the estuary. The combined effect of temperature and salinity was more important than the single factors in predicting species occurrence. The same was found in the Severn estuary (UK), where the presence of euryhaline species like whiting, flounder and bass was related with times or areas where salinity was relatively high (Potter *et al.* 1997).

Cross-validation with part of the data sets and with randomly generated values for the 4 environmental variables, proved the models to be accurate and robust (Chapter 6). Also, it was shown that the logistic models that were developed for the Westerschelde were capable of predicting the occurrence (presence/absence) of several demersal fish and macro-crustaceans in the Oosterschelde (see Chapter 6 Addendum). Although for a number of species the absence could not be predicted well, and the presence/absence models generally failed to predict the absence of species like brown shrimp *Crangon crangon* (also in the Westerschelde) and shore crab *Carcinus maenas*, as these species were present almost everywhere and throughout the year in Oosterschelde.

From the presence/absence models, it can be concluded that, next to species diversity, also species occurrence is dominated by a seasonal rather than a spatial pattern. This might explain why most models could be successfully applied to the Oosterschelde, where no marked salinity/turbidity gradient exists.

9.6 Density patterns

9.6.1 The multivariate (multispecies) approach

The relation between the environmental variables and species abundance at the community level has been tackled since the 1980s by a whole battery of multivariate statistical techniques, either by means of direct or indirect classification or ordination, all with their own pros and cons (James & McCulloch 1990). These techniques created the possibility of summarizing the structural patterns in large multispecies data sets (see Chapter 2-Add.2, Chapter 3-Add.).

In the quantitative description of fish communities, numerical data are most commonly used as abundance measure, and in most situations the choice between numbers and biomass in multivariate analyses matters little (Bianchi & Høisæter 1992). Throughout the different chapters of this thesis on structural patterns (PART I), both density and biomass data were presented and in most cases they yielded the same results when characterizing the

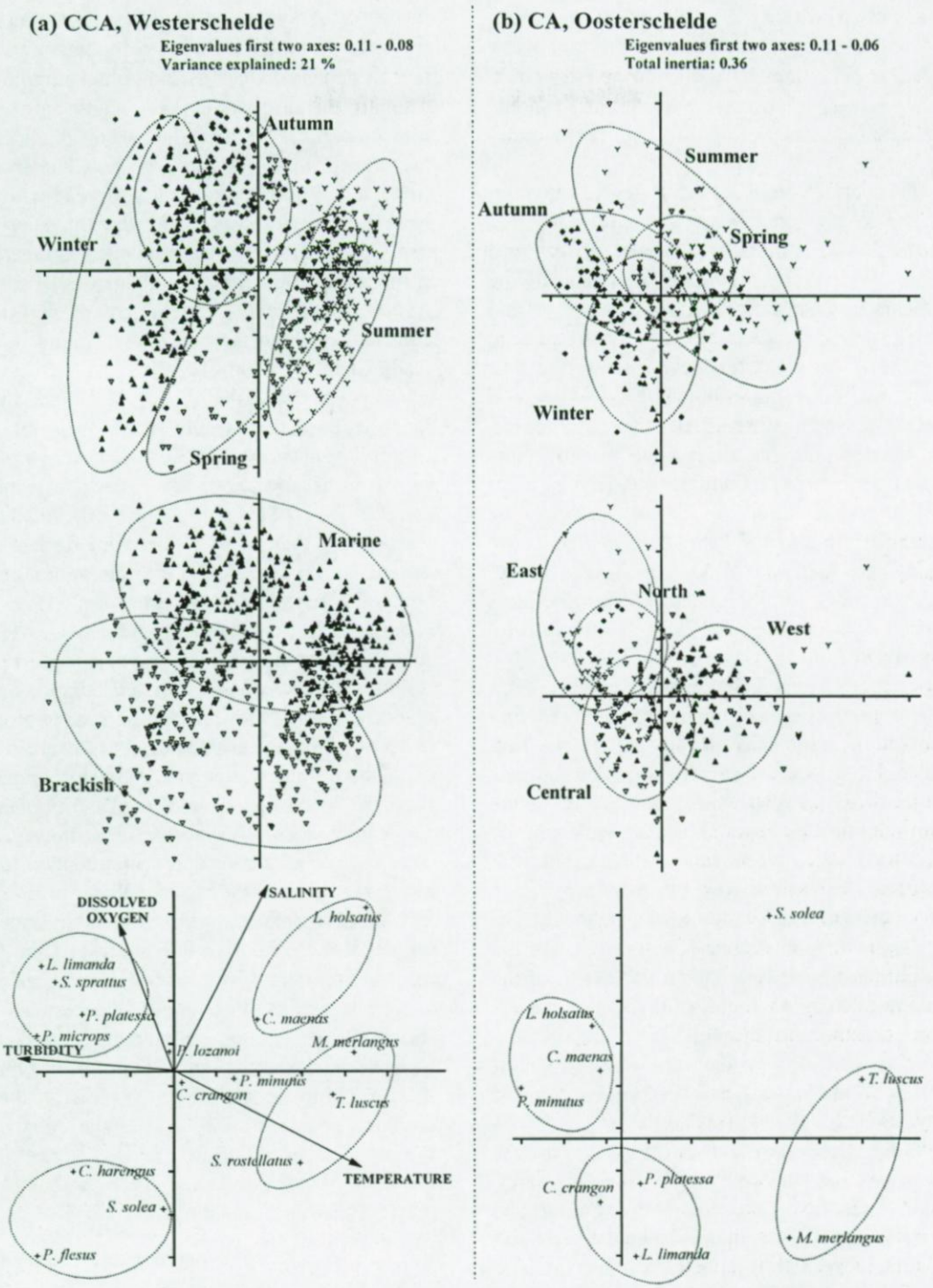


Fig. 9.8 Sample and species(-environmental) scores in the plane of the first two axes, representing seasonal and spatial multi-species responses as a result of (a) Canonical Correspondence Analysis with the Westerschelde data (15 species, 730 sampling points, 4 environmental variables), and (b) Correspondence Analysis with the Oosterschelde data (9 species, 255 sampling points)

demersal fish and macro-invertebrate assemblages. Data reduction through elimination of rare species may alleviate the inordinate amount of zero observations (Field *et al.* 1982).

Canonical Correspondence Analysis (CCA) is now probably the most widely used multivariate direct gradient analysis method in community ecology (Palmer 1993). As the ordination of samples and species is constrained by their relationships to only a few environmental variables, this type of analysis presumes that meaningful environmental variables are measured. In other words: though a direct gradient analysis facilitates interpretation, the results from the CCA should not deviate much from the pure community gradients shown by CA (Correspondence Analysis) or RA (Redundancy Analysis). Although not always made that clear, many more multivariate analyses were performed for the different studies

than those shown, where the results of different classification and ordination techniques were compared, following the guidelines as indicated in Chapter 2-Add.2. Moreover, multivariate techniques should only be used as descriptive tools in exploratory analyses.

Multivariate analyses on the whole assemblage of the Westerschelde are given in Chapter 2 and Chapter 2-Add.1; on both estuaries in Chapter 3 en Chapter 2-Add.2; on the fish assemblage of the Oosterschelde in Chapter 3-Add. and Chapter 4; and on the macro-invertebrate assemblages in Chapter 5. In this synthesis, the CCA for the Westerschelde was constrained by the 4 environmental variables, and based on 4^{th}-root transformed density data for 15 common species gathered during the monthly surveys in the period 1988-'91 and the quarterly surveys in August 1999- May 2000. As for the Oosterschelde not enough environmental data were gathered, the Correspondence Analysis (CA) was based on the quarterly data for 9 common species, from the periods August 1987 – November 1989 and August 1999 – November 2001.

For the Westerschelde, a seasonal separation in warmer and colder seasons was shown, mainly related to temperature and turbidity, along the first axis (Fig. 9.8a). A spatial segregation between marine and brackish samples (see Fig. 9.1) along the second ordination axis was correlated with salinity and dissolved oxygen. According to their position in the plot of the 2 canonical axes, the species could be classified as typical brackish or marine, typical summer or winter, or indifferent species. Almost the same seasonal patterns were shown in the CA of the Oosterschelde, where the allocation of the species was even more correlated with the corresponding seasonal quadrants (Fig. 9.8b). The aggregation of the sampling points in a western, central, eastern and northern group (cf. Fig. 9.1) was less clear.

As has been shown with the single species response curves and surfaces, the relation with salinity, turbidity, dissolved oxygen concentration and temperature in the Westerschelde seemed quite obvious. The same correlations have been found in many other estuaries (*e.g.* Henderson 1989, Thiel *et al.* 1995, Cyrus & Blaber 1992, Whitfield 1999). For example, in the Humber estuary (UK), the same correlations were found with temperature, salinity and oxygen, but not with turbidity (Marshall & Elliott 1998). However, Potter *et al.* (1997) concluded that the species composition in the Severn estuary (UK) was not related with either salinity or water temperature. Also, in the Oosterschelde the relation with salinity was probably of less importance.

It was suggested by Maes (2000) that pooling monthly data often produces trivial correlations and that there exists no causal relation between fish distribution and the environment. In the present study, the low eigenvalues and the low percentage of the variance explained could be partly attributed to the large variation, introduced in the analyses by taking all density values as individual sampling points. Though, the results were in general agreement with previous studies, where data were averaged exactly to reduce this variation (*e.g.* Chapter 2-Add.2, Chapter 2). Moreover, clear differences in densities were noted within and between the Westerschelde and Oosterschelde estuaries, which is clearly related with the environmental characteristics of the systems. Also, between the Grevelingen and Oosterschelde ebb-tidal deltas differences were found (Chapter 4-Add., Chapter 2-Add.2).

The definition of ecological guilds within the functional guild concept, which was optimized by Elliott & Dewailly (1995), is nowadays widely accepted to describe common patterns of estuarine usage (see Elliott & Hemingway 2002). In Chapter 2, it was shown that species could be further classified dependent on the period of maximum abundance, both on a temporal and spatial scale. For example, some species are typically summer-early autumn species preferring marine waters (*e.g.* bib *Trisopterus luscus,* whiting *Merlangius merlangus* and flying crab *Liocarcinus holsatus*); others were more or less resident in the Westerschelde, but occurred at higher densities during winter in the brackish reaches (*e.g.* herring *Clupea harengus*, flounder *Platichthys flesus* and common goby *Pomatoschistus microps*); others were typical winter species which tended to occur at moderate salinities (*e.g.* plaice *Pleuronectes platessa* and dab *Limanda limanda*). The same patterns were reflected in the multivariate analyses (Fig. 9.8). The most common and estuarine resident species, which occurred almost throughout the estuary (brown shrimp *Crangon crangon*, sand goby *Pomatoschistus minutus* and lozano's goby *Pomatoschistus lozanoi*), were found in the middle of the plots for the Westerschelde. The lack of typical estuarine gradients in salinity and turbidity in the Oosterschelde mainly explains why the seasonal patterns in the fish and macro-crustacean assemblage were clearer than the spatial patterns.

9.6.2 Spatial and long-term patterns

Another way of looking at patterns in community structure is by means of a simple graphical method. The thesis largely benefits from the fact that two different periods with a separation of 10 years could be compared. In the following paragraphs, both spatial and long-term patterns in the overall fish and macro-invertebrate assemblages within and between the Westerschelde and Oosterschelde estuaries are discussed. For comparative reasons, only part of the density data are used, based on the quarterly surveys for the periods February 1988 – November 1989 and February 2000 – November 2001.

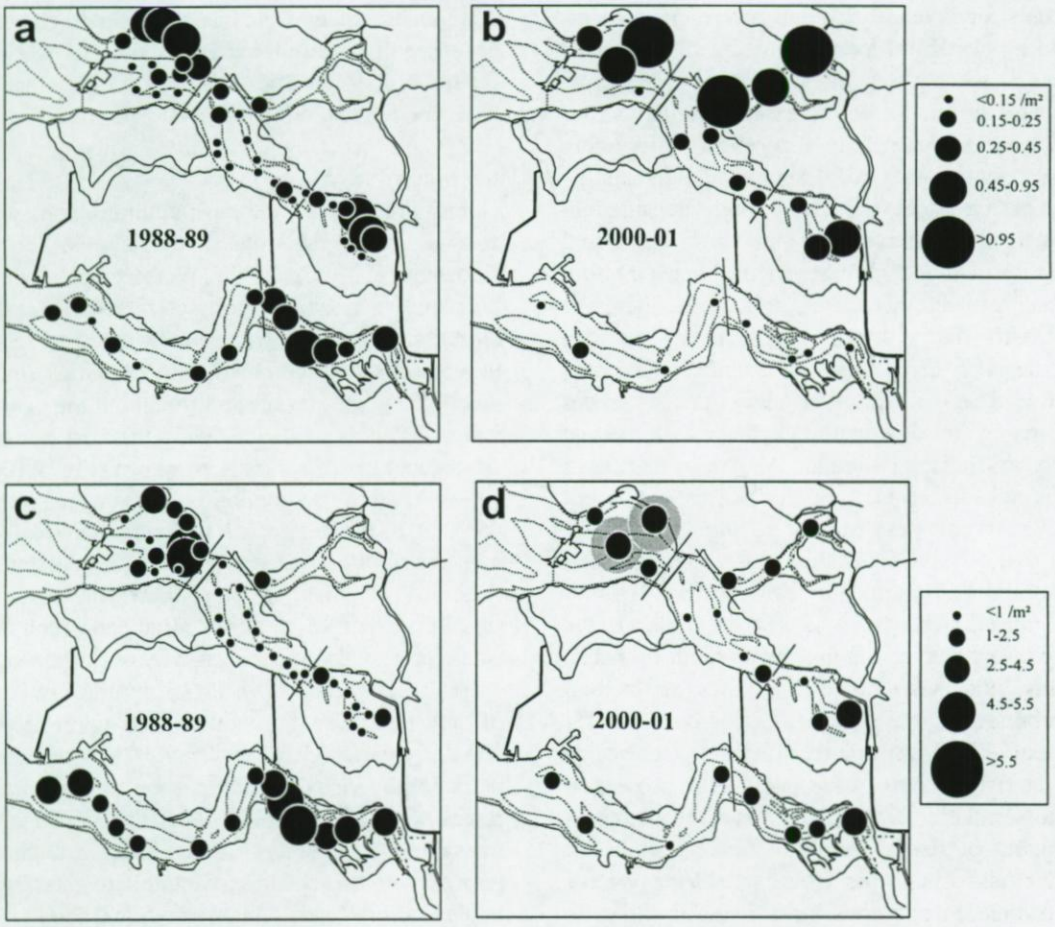


Fig. 9.9 Spatial and long-term patterns in total average densities for the fish (a,b) and macro-invertebrate (c,d) communities in the periods 1988-'89 and 2000-'01 in the Westerschelde and Oosterschelde estuaries. Note the different scales for fish and macro-invertebrates. The grey circles include average densities for ophiuroids, which were not investigated during the first period

At the end of the 1980s, total average densities were higher in the brackish part of the Westerschelde, both for the fish (on average 0.4 ind m^{-2}) and macro-invertebrates (on average 4 ind m^{-2}) (Fig. 9.9). The overall dominance of a few macro-invertebrate species (an order of magnitude higher than all fish species together) has been noted for most, if not all, shallow estuarine and coastal areas (overview in Elliott & Hemingway 2002).

At the beginning of 2000, average densities were much lower for both fish (on average 0.1 ind m^{-2}) and macro-invertebrates (1.6 ind m^{-2}), and more or less comparable between the two zones in the Westerschelde estuary. In the Oosterschelde, average fish densities were lowest in the central part (on average 0.4 and 0.9 ind m^{-2}) in both periods, and higher in all subareas in 2000-'01 (on average 1.9 ind m^{-2} in the western, eastern and northern part). Macro-invertebrates densities were a little higher throughout the Oosterschelde in 2000-'01, and were highest in the western part (on average 1.9 and 3.5 ind m^{-2}) in both periods. Total average fish and macro-invertebrate densities were comparable in several subareas between both estuaries in 1988-'89, while this was only the case for macro-invertebrates in 2000-'01. Average fish densities were almost an order of magnitude higher in the latter period in the Oosterschelde compared to the Westerschelde.

From these graphs one might conclude that fish and macro-invertebrates are doing relatively well in the Oosterschelde, while the role of the Westerschelde as a nursery has decreased at the beginning of the 21th century. In the Tagus estuary (Portugal), a decreased abundance of many juvenile fish species (*e.g* bib *Trisopterus luscus*, rockling *Ciliata mustela*, and flounder *Platichthys flesus*) was noted from 1978-'80 towards 1994-'96, which was mainly attributed to pollution, fishery regulation and water-flow control (Costa & Cabral 1999).

Next to the extraction of sand (yearly 3 10^6 m^3), dredging the main shipping channel and dumping of the dredged material in the Westerschelde has continuously increased during the past 40 years from 2 to 10 10^6 m^3 per year, and mainly takes place in the brackish part (Mol *et al.* 1997). For the recent deepening 48'/43', even >16 10^6 m^3 per year was (and will be) dredged (Anonymous 1998). Both activities lead to a reduction of the shallow subtidal and intertidal habitats (erosion of the flats and filling of the marsh creeks), which are necessary foraging areas

and refuges for juvenile fish and macro-crustaceans. Independent of habitat loss, changed sediment characteristics (coarser sand and more shell fragments) and disturbance due to the increased dredging activities during recent years, may also have contributed to the lower densities in 2000-'01 in the Westerschelde.

On the other hand, the high densities in 2000-'01 in the Oosterschelde may partly be related to net efficiency and conversion problems. During several surveys in this latter period, the net was clogged with macrophytes, which may have increased the net efficiency for smaller organisms (Chapter 4). These allochtonous algal mats also seem to be of major concern for the harvesting of mussels in the Oosterschelde. To reduce the risk of tearing or losing the net (due to high amounts of oysters, mud, macrophytes, tunicates) mainly in the eastern and northern part of the Oosterschelde, the sampling distance was reduced from 1000 to 500 m and sometimes to 300 m during most surveys in 2000-'01 (see Chapter 5). The conversion to a standard unit surface, will surely have led to overestimations of the real densities present in these subareas. Moreover, natural inter-annual variability partly obscures long-term changes in fish density. Additionally, the protection of the Oosterschelde as nature reserve and the complete banning of fishing activities (except shell and recreational fishery) in the Oosterschelde may have created favorable conditions for growing up juvenile fishes.

9.6.3 Seasonal patterns per taxonomic group

While Chapters 2 and 3 mainly focused on the 1980s, the comparison between seasonal, spatial and long-term patterns in density, biomass and growth for the different taxonomic groups at the end of the 1980s and 1990s, has been extensively discussed in Chapters 4 and 5.

As the ecological guild concept is used to describe the seasonal patterns, it may be necessary to explain the terms used: ER- estuarine resident species, which spend their entire lives in the estuary; MJ – marine juvenile migrant species, which use the estuary as a nursery and spend the rest of their life at sea; MS – marine seasonal migrants species, which regularly visit the estuary as adults; MA – marine adventitious visitors or stragglers, which can appear in the estuary, with no apparent estuarine requirements; CA – catadromous/anadromous migrant species, which pass through the estuary between their spawning and feeding areas; FW – freshwater adventitious species, which occasionally enter the estuary (Elliott & Dewailly 1995).

The following paragraphs are again based on the quarterly density data from the periods 1988-'89 and 2000-'01. Although, Fig. 9.10 and Fig. 9.11 contain a lot of information on spatial and long-term patterns as well, mainly the seasonal patterns for the commonest species within the different taxonomic groups will be discussed here. The possible reasons for the higher densities in 2000-'01 for most groups have been given in the previous paragraph.

Gobiidae

Gobies are amongst the most common fish species in coastal and estuarine habitats (Miller 1986, Hamerlynck 1990). In the Westerschelde, three gobiid species Lozano's goby *Pomatoschistus lozanoi* (MA), sand goby *Pomatoschistus minutus* (ER), and to a lesser extent common goby *Pomatoschistus microps* (ER), were common throughout the year, but at lower densities in spring when the first two species are located in deeper water to spawn (Fig. 9.10a).

Although six gobiid species were recorded in the Oosterschelde, only *P. minutus* was really common during the same seasons as in the Westerschelde (Fig. 9.11a). Also, in other European estuaries *P. lozanoi* seemed to be only sporadically recorded and was therefore categorized as MA (e.g. Pomfret *et al.* 1991, Thiel *et al.* 1995). Probably, the low densities of mysids (Chavatte 2001), its preferred prey (Hamerlynck & Cattrijsse 1994, Chapter 7) and the predation by visual predators such as bib *Trisopterus luscus* (Chapter 7-Add.) due to the high water transparency in the Oosterschelde, are the main reasons why this species is not able to establish itself in the Oosterschelde (Chapter 2-Add.2).

Pleuronectiformes

Estuaries are important nurseries for flatfish (*e.g.* van der Veer *et al.* 1990b, Henderson & Seaby 1994). In terms of biomass they are the most important group of fishes (Chapter 3, Chapter 4). Of the eight species, three species are common in both estuaries, all with higher densities in the brackish part of the Westerschelde, and in the western and northern part of the Oosterschelde (Fig. 9.10b). Dab *Limanda limanda* (MJ) was the commonest species in the Westerschelde, but only present in autumn-winter. Also, plaice *Pleuronectes platessa* (MJ) was mainly recorded in autumn-winter.

In the Oosterschelde, plaice was the commonest species, and both plaice and dab were abundant throughout the year (Fig. 9.11b). In the period 1969–'78, before the engineering works in the Oosterschelde, dab showed more or less the same density pattern as in the Westerschelde (De Veen *et al.* 1979). As the Oosterschelde was altered from a real estuary into a marine bay, dab (and plaice) densities in 1988-'89 and 2000-'01 resembled a coastal pattern, comparable to that in the shallow ebb-tidal delta of the Grevelingen (Chapter 4-Add.). In shallow subtidal coastal areas, small juveniles arrive earlier at higher densities and especially larger individuals (1 and 2 group) stay longer in the ecosystem during springtime (Chapter 4-Add.). In winter two cohorts of *L. limanda* and *P. platessa* could be detected,

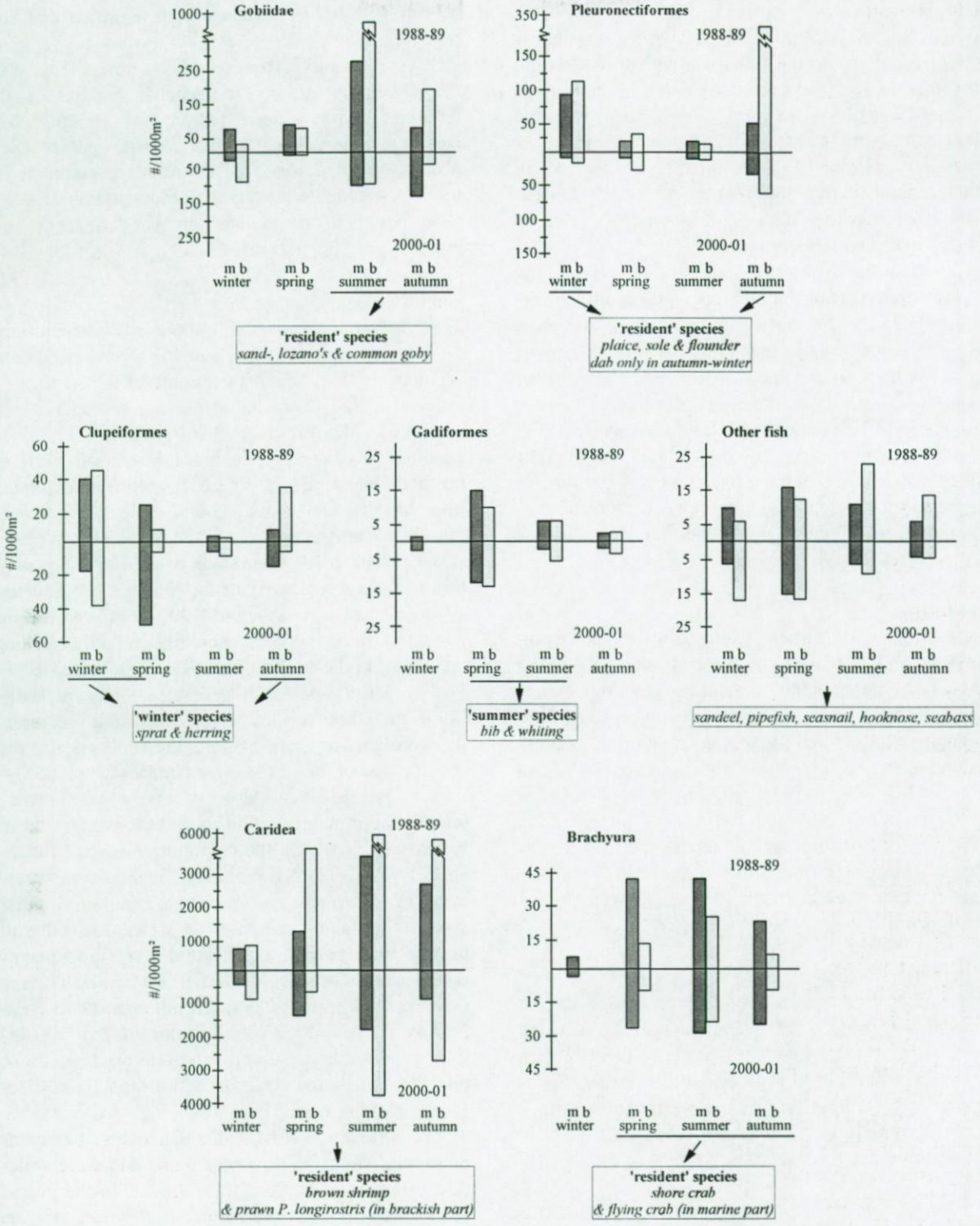


Fig. 9.10 Seasonal, spatial and long-term patterns in average densities per taxonomic group in the periods 1988-'89 (upper part of the graphs) and 2000-'01 (lower part) in the Westerschelde estuary; subareas: marine (m) and brackish (b). An indication of the main species is given

which was in accordance with observations in the estuaries on the west coast of Scotland as well as in the Wadden Sea (Elliott *et al.* 1990).

Although, 22 % of the juvenile sole *Solea solea* (MJ) population in the Dutch coastal waters are located in the Delta area, this species was recorded in lower numbers in both estuaries, compared to plaice and dab. As *S. solea* prefers muddy substrates (*e.g.* Marchand 1988), a 3-m beam trawl with only 1 tickler chain, may not be efficient enough to catch this species. Flounder *Platichthys flesus* (ER/CA) was present throughout the year in lower numbers in both estuaries.

Clupeiformes

Of the 4 clupeoid species only 2 species are really common in both estuaries, with sprat *Sprattus sprattus* (MS) mainly present in autumn and winter (Fig. 9.10c and Fig. 9.11c). Herring *Clupea harengus* (MJ) was more common than sprat (except for the period 1988-'89 in the Westerschelde), also occurring mainly in the colder months in the Oosterschelde, but with a shift towards winter and early-spring in the Westerschelde.

In the Thames estuary (UK) peak abundances of herring and sprat were found in December-March, which was correlated with high dissolved oxygen concentrations and low temperatures (Power *et al.* 2000a). Gobies, nilsson's pipefish *Syngnathus rostellatus*, and clupeoids were the only important groups in the Zeeschelde (Belgium), where pipefish arrived in summer, gobies in late fall and juvenile clupeoids in early winter (Maes *et al.* 1998a). No explanation was found for the high density peak of *C. harengus* in summer in the northern part of the Oosterschelde.

Gadiformes

Of the four gadoid species, only 2 species are common in both estuaries, with bib *Trisopterus luscus* (MJ) twice as abundant as whiting *Merlangius merlangus* (MJ). They are typical 'summer' species, with 0-group whiting mainly present in spring, and bib extending its occurrence till summer (Fig. 9.10d and Fig. 9.11d). Although 1+ individuals were recorded in low numbers throughout the year.

Both gadoid species are an important ecological component of shallow coastal waters and estuaries (Claridge & Potter 1984), and were extensively studied in many areas (Chapter 7-Add.).

Other fish species

Most other fish species are less common, with the exception of nine species (5 in each estuary) which are almost all classified as estuarine resident species (Fig. 9.10e and Fig. 9.11e). Nilsson's pipefish *Syngnathus rostellatus* (ER) was mainly found in spring-summer, mainly in the brackish part of the Westerschelde and not from the western part of the Oosterschelde.

Dragonet *Trigla lucerna* (MJ), viviparous blenny *Zoarces viviparus* (ER) and butterfish *Pholis gunnellus* (ER) were mainly recorded from the Oosterschelde, throughout the year, with dragonet mainly in summer-autumn, viviparous blenny almost not in the eastern part, and butterfish almost not in the western part.

Sandeel *Ammodytes tobianus* (ER) and seasnail *Liparis liparis* (ER) were mainly recorded from the Westerschelde. Sandeel was found throughout the year, but more in winter in 1988-'89 and more in the marine part in 2000-'01. Seasnail is a typical bimodal species with higher densities both in spring and autumn (Chapter 2).

Bull-rout *Myoxocephalus scorpius* (ER) was more common in the Oosterschelde, but less in autumn and with a decreased density in 2000-'01. Hooknose *Agonus cataphractus* (ER) and seabass *Dicentrarchus labrax* (MJ) were more common in the Westerschelde during the colder months, hooknose mainly in the marine part and seabass in the brackish part, but not in 1988-'89.

Caridea

Three caridean shrimps were recorded of which only 1 in the Westerschelde. Brown shrimp *Crangon crangon* (ER) is the most common macro-crustacean species in both estuaries, occurring throughout the year at high densities (Fig. 9.10f and Fig. 9.11f). It is commercially fished on the North Sea coasts, with an average annual landing of 2.6 10^4 tonnes (consumption shrimps) between 1995 and 2000 (Anonymous 2001). Although, the contribution of the Westerschelde to the exploitable stock of the North Sea may be rather low compared to the Dutch coast and the Wadden Sea (Anonymous 2001), the juvenile population in the Westerschelde is probably a major contibutor to the adult stocks in the Belgian coast.

The lower densities of *C. crangon* in 1988-'89 in the Oosterschelde were related to a temporarily disturbed distribution during the 1980s, due to the construction of the storm-surge barrier (Chapter 5).

The nine caridean prawns in the Oosterschelde were mainly found in autumn-winter and in the eastern part, with the commonest species *Palaemon adspersus* (MS), probably related to the presence of green macro-algae and seagrasses (Pihl 1986). This 'alien' species clearly took the niche of other prawn species, as till the 1980s *P. adspersus* was almost not caught in the Dutch Delta area (Adema 1988). Also, *Pandalus montagui* (MS), *Palaemon elegans* (MS) and *Palaemon serratus* (MS) were of some importance in the Oosterschelde, also related to sediment and vegetation type (Heerebout 1974, Smaldon *et al.* 1993). Probably, the abundance of the caridean prawns will be underestimated, as these species are more likely to be found on other than soft substrates.

In the Westerschelde, 2 caridean prawns were recorded, but only white shrimp *Palaemon longirostris* (MS) was of some importance, mainly in spring-summer and in the brackish part. This species was probably not present in 1988-'89 (Mees *et al.* 1995). The re-occurrence of *P. longirostris* in the Westerschelde is probably related to an improved water quality. In the lower Zeeschelde (Belgium) this species was replaced by *Palaemonetes varians*, which together with *C. crangon*, were the only macro-invertebrates of importance in the upper part of the Schelde estuary (Maes *et al.* 1998a).

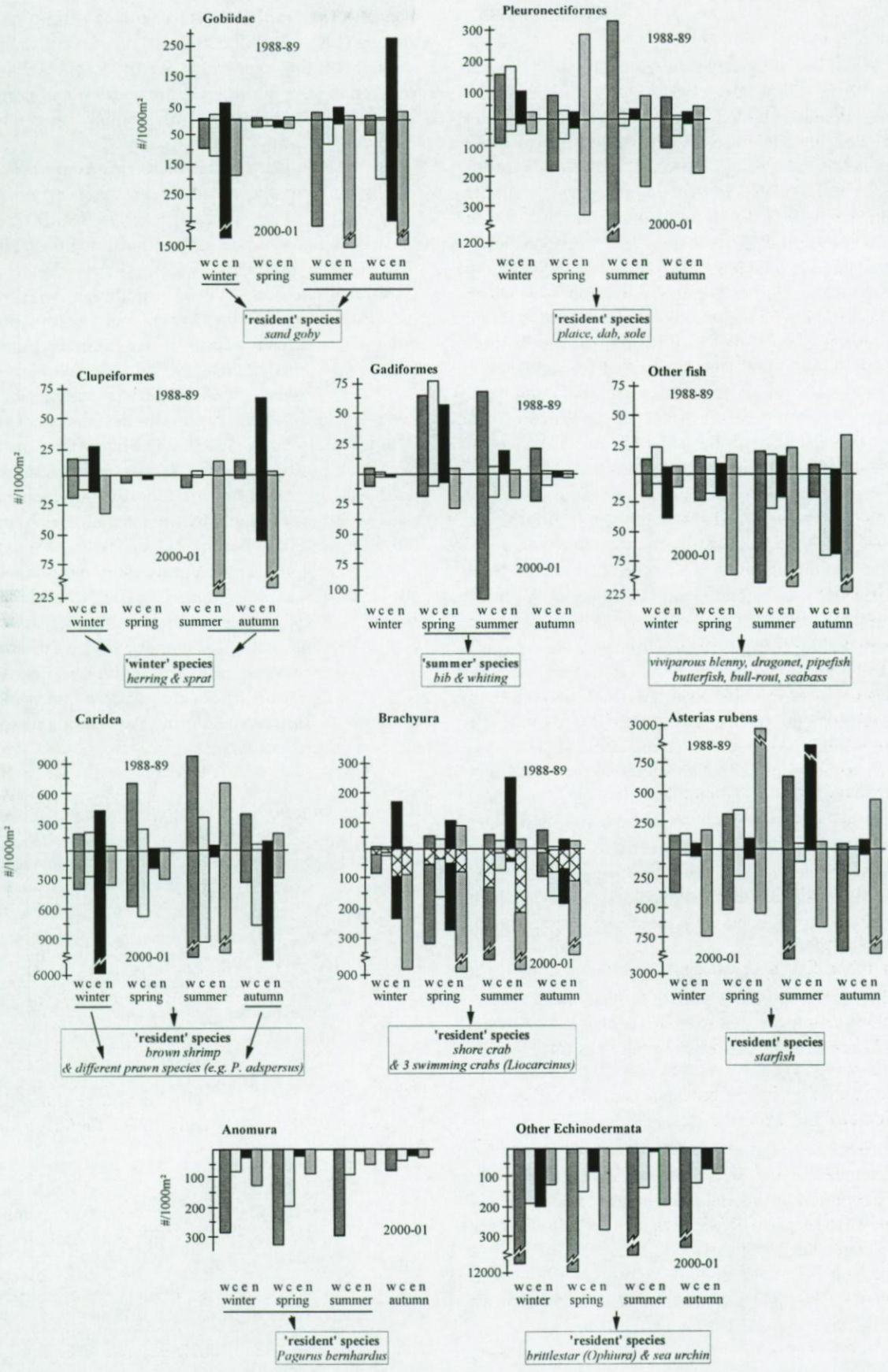


Fig. 9.11 Seasonal, spatial and long-term patterns in average densities per taxonomic group in the periods 1988-'89 (upper part of the graphs) and 2000-'01 (lower part) in the Oosterschelde estuary; subareas: western (w), central (c), eastern (e) and northern (n). An indication of the main species is given. Hatched bars for the Brachyura include crab species, which were not investigated during the first period

Brachyura

Of the 10 brachyuran species, only 3 species were recorded in the Westerschelde and 9 species in the Oosterschelde, with an overall dominance of shore crab *Carcinus maenas* (ER) throughout the year. *C. maenas* has been found to be common in other estuaries as well, related to substratum type, *e.g.* higher production in areas with musselbeds on the Swedish west coast (Pihl & Rosenberg 1982). This species is well adapted to adjust its apparent water permeability in response to decreased salinities (Rainbow & Black 2001), which explains why this species is also found in high numbers in the brackish part of the Westerschelde (Fig. 9.10g). The presence of berried females of *C. maenas* throughout the year (but mainly in spring), was in agreement with the presence of different brood waves in the shallow coastal waters in Sweden (Pihl & Rosenberg 1982).

Flying crab *Liocarcinus holsatus* (MJ/ER) was mainly present in spring-summer in the marine part of the Westerschelde, while together with arch-fronted swimming crab *Liocarcinus arcuatus* (ER) and harbour crab *Liocarcinus depurator* (ER), these swimming crabs are found throughout the year in the Oosterschelde (Fig. 9.11g). However, *L. holsatus* reached highest densities in the western part, while *L. depurator* was mainly recorded from the northern part. The latter species only started to colonize the Oosterschelde since 1990 (Adema 1991b). This spatial separation was probably related to their sediment preferences. The successful invasion of *L. arcuatus* since 1982 may be related to its herbivorous feeding habits (Adema 1991a). Moreover it is the only crab species with a changed sex ratio from 1:1 to 3:1 females over males during the colder seasons, which could be advantageous for a rapid population growth (Chapter 5).

The spider crab *Macropodia rostrata* (MS) was of some importance in the Oosterschelde, mainly in summer, but the densities are probably underestimated, as this species prefers rough substrates (Wolff & Sandee 1971).

Anomura

Two species of hermit crabs were recorded in the Oosterschelde, with only *Pagurus bernhardus* (ER) being common throughout the year, but mainly found in the western part (Fig. 9.11i). This group was only investigated in 2000-'01. The absence of hermit crabs from the Westerschelde is probably related to the lack of suitable gastropod shells, rather than to salinity preferences (Chapter 5).

Echinodermata

Most echinoderms prefer higher salinities, which probably explains the absence of this group in the Westerschelde (Wolff 1968). Six species of echinoderms were found in the Oosterschelde, but only starfish *Asterias rubens* (ER) and brittlestar *Ophiura* species (ER) (*O. ophiura* and *O. albida*) are abundant throughout the year (Fig. 9.11h & j). *A. rubens* reached highest densities in the western and northern part, while *Ophiura* were only common in the western part.

The high densities of *A. rubens* are probably correlated with the abundant presence of its main food source, blue mussel *Mytilus edulis* in the Oosterschelde (Guillou 1996, Smaal & Lucas 2000). The absence of starfish in the Westerschelde may also be related to industrial pollution with polychlorinated biphenyls (PCB) and heavy metals (Cadmium), which seem to affect their reproduction (den Besten 1991, Chapter 2-Add.2).

O. ophiura prefers soft sediments and has been found in thick layers in several areas (*e.g.* (Wolff 1968, Aronson 1989). The success of the brittlestars is probably related to a series of successive mild winters at the end of the 1990s, which has a positive effect on the high interannual variability of these species (Leewis *et al.* 1994).

The other echinoderms *Echinocardium cordatum*, *Psammechinus miliaris* and *Ophiothrix fragilis* were only of limited importance. *E. cordatum* was mainly present in spring-summer in the western part. The other two were recorded throughout the year, with *P. miliaris* mainly in the western and northern part, and *O. fragilis* mainly in the eastern and northern part of the Oosterschelde.

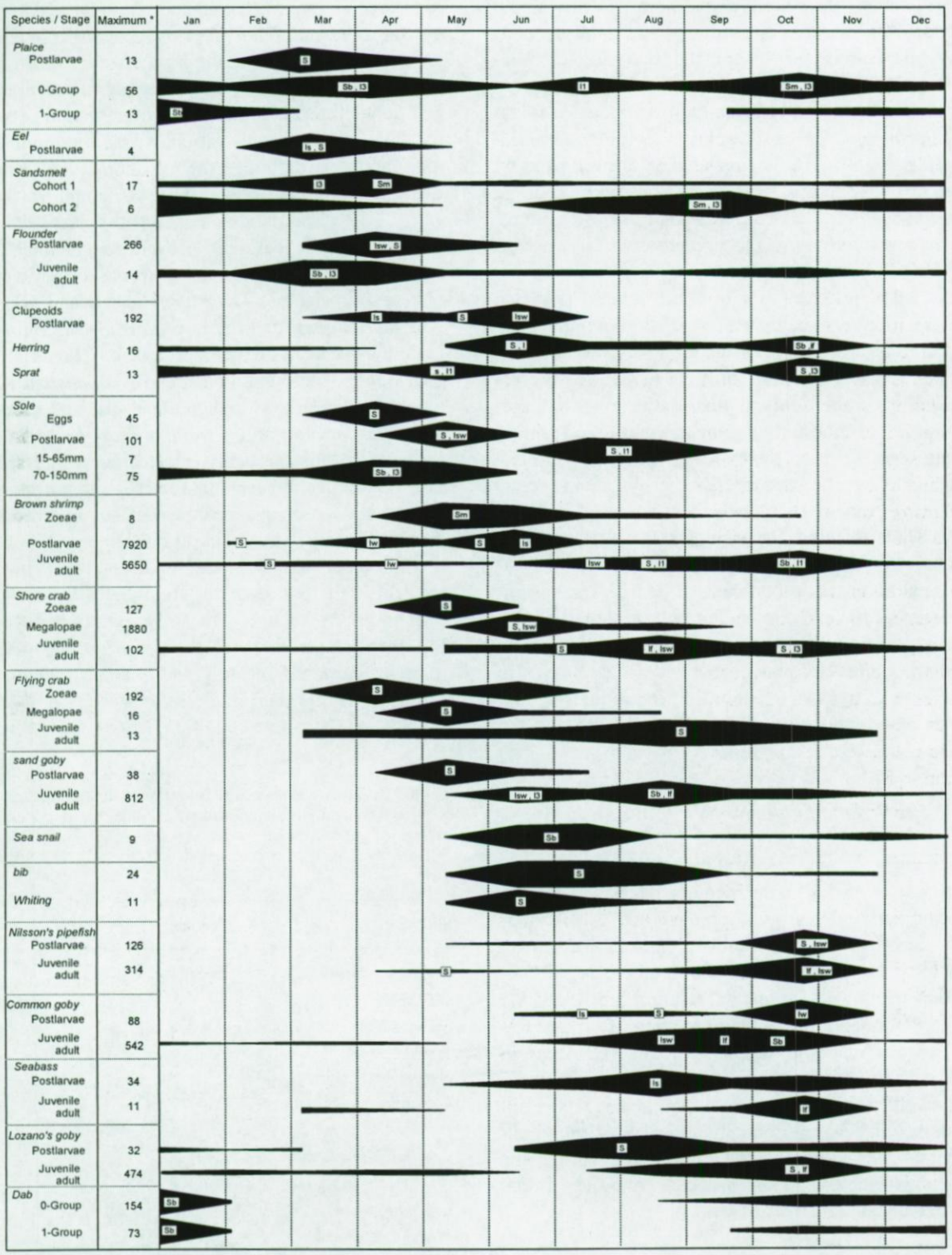
9.6.4 Seasonal patterns throughout the early history

In conclusion of the previous paragraph, it has been shown that estuarine residents (ER) and marine juveniles (MJ) are the commonest species in both estuaries, sometimes with a preference for a certain part of the estuaries. Also, only few species are really abundant as well in the Westerschelde as in the Oosterschelde. Many marine seasonal or adventitious species (MS/MA) increased the biodiversity of the fish and macro-invertebrate assemblages, but these are usually found in low numbers during different part of the year, and mostly in the higher salinity reaches. Only one freshwater (FW) species and only six catadromous species (CA) were recorded in the Westerschelde during the study period described in these paragraphs. More or less the same conclusions were drawn for several other european estuaries (see Elliott & Hemingway 2002).

Moreover, not only the subtidal, but also the other subhabitats of an estuary are inhabited during different periods, by different species and several life stages of fish and macro-invertebrates. In the following paragraphs, a combination of the (post)larval appearance and the juvenile/adult life stages of 17 common species, is presented for the Westerschelde estuary. This summarizing graph (Fig. 9.12) is based on subtidal data from the marine and brackish zones

gathered between 1988-'91, intertidal data gathered in 1992 at 2 different depths (MTL –1 m and –3 m) on the brackish intertidal flat of Valkenisse-Walsoorden, and intertidal data gathered in 1990-'91 in two brackish saltmarsh creeks (Saeftinghe and Waarde) (see Chapter 1, and Fig. 9.1). More details are given in Hostens *et al.* (1996) and in Chapter 2. More or less the same patterns were found for the fish and macro-invertebrate assemblages in the Oosterschelde (see Chapter 4, Chapter 5).

First of all, a clear succession of the different life stages per species can be seen, from egg or larvae, over postlarvae to juvenile O-group and juvenile 1-group individuals (Fig. 9.12). Secondly, a seasonal



° (The largest width of the kites agrees with the given maximum density (#/1000m²) per species, averaged per month (1988-1992) for all subhabitats)
Subtidal (S) marine (Sm) and brackish (Sb), Intertidal (I) flat (If) -3m stratum (I3) and -1m stratum (I1), intertidal saltmarsh creek Saeftinghe (Is) and Waarde (Iw)

Fig. 9.12 Summarizing scheme on the seasonal appearance of different early-life history stages of 17 common species in different subhabitats of the Westerschelde, with an indication of the subhabitats where the life stages were recorded with the highest densities

succession of different species is shown, where post-larvae of plaice *Pleuronectes platessa* and eel *Anguilla anguilla* and the smallest juveniles of sandeel *Ammodytes tobianus* already appear in February (late-winter) in the Westerschelde. Most of the species appear in early-spring, like brown shrimp *Crangon crangon*, shore crab *Carcinus maenas*, swimming crab *Liocarcinus holsatus*, flounder *Platichthys flesus*, herring *Clupea harengus*, sprat *Sprattus sprattus*, sole *Solea solea* and sand goby *Pomatoschistus minutus*. Others appear for the first time in late-spring, like seasnail *Liparis liparis*, bib *Trisopterus luscus*, whiting *Merlangius merlangus*, seabass *Dicentrarchus labrax* and lozano's goby *Pomatoschistus lozanoi*. These species then are followed by a number of species, which appear in summer in the Westerschelde, like nilsson's pipefish *Syngnathus rostellatus*, common goby *Pomatoschistus microps* and dab *Limanda limanda*.

Highest densities of (post)larvae for brown shrimp, flounder, clupeoids, pipefish, common goby and seabass are recorded from the intertidal saltmarsh creeks. Highest densities of most juveniles were recorded from the subtidal and/or the intertidal flat. Although, estuarine resident species are present throughout the year, several species show a preference for either the warmer (summer-resident species) or colder seasons (winter-resident species). Most of the marine juvenile species appeared at varying times (summer, winter or bimodal), but most of the O-group cohorts reach their highest densities in spring-summer and often remain for only a short time. A number of species are more common in summer-autumn, while dab, plaice, sole and sandeel, are also represented by a 1+ cohort during winter-spring. Older individuals are only occasionally noted in the estuary.

9.6.5 Prediction of abundance

Clear seasonal and/or spatial patterns in density (and biomass) of the different demersal fish and macro-invertebrate species were pointed out. Also, long-term density patterns in both estuaries were shown. Single-species models can contribute to reveal important species-environmental relationships (Attrill *et al.* 1999). In addition to the prediction of occurrence, it was also tried to predict patterns (changes) in abundance of 15 common species. This was done by means of single species multiple linear regression models, with 4 environmental variables and their quadratic derivations as the forcing effects, and the log-transformed (ln+1) density data from the subtidal Westerschelde (Chapter 6).

Although most density models agreed with the actual distribution of the species, these models generally failed to predict extreme peaks and troughs, which is not uncommon to data series that fluctuate through several orders of magnitude (Nisbet & Gurney 1982). In accordance with the presence/absence models, both temporal and spatial patterns were predicted, but the different models could only explain between 20-55 % of the variance (Table 9.2).

Best models were built for those species that were present in the estuary for a longer period, but with only one clear density peak in either a cold or a warmer season (see previous paragraph). In decreasing order of variance explained, these were the models for *Limanda limanda, Pomatoschistus microps, Carcinus maenas, Liocarcinus holsatus, Platichthys flesus, Sprattus sprattus and Pomatoschistus minutus*. It is concluded that the combined interaction between the four environmental variables was the main forcing factor structuring the temporal and spatial distribution of these seven species (Chapter 6).

The least models concerned species belonging to the ecological guild of 'marine juveniles', *i.e.* species that either were present in the estuary during only a short period (*Trisopterus luscus* and *Merlangius merlangus*), or to species with higher densities in both a warmer and a colder season (*Clupea harengus, Solea solea* and *Pleuronectes platessa*). Also, the density models for *Syngnathus rostellatus, Pomatoschistus lozanoi* and *Crangon crangon* were less successful. Most probably, the temporal and spatial distribution of the latter eight species was more governed by the proper appearance of suitable food resources (Hemingway & Elliott 2002).

In a next step, the six best-fitting models were applied to a data set from the Oosterschelde (Chapter 6 Addendum). These were mainly successful when temperature was the main forcing variable (e.g. for *Sprattus sprattus* and *Pomatoschistus microps*). The constant high salinity in the Oosterschelde is a favorable condition for *Carcinus maenas*

Table 9.2 Variance explained (R^2) for the 15 density models, and the selected environmental variables (and/or the quadratic effects) in order of importance per model: temperature (T, T^2), salinity (S, S^2), dissolved oxygen concentration (O, O^2), and turbidity (Tu, Tu^2)

Species	R^2	Variables
Clupea harengus	0.33	S, S^2, Tu^2, T
Sprattus sprattus	0.50	T, T^2, O^2, O, S, Tu
Merlangius merlangus	0.32	Tu, Tu^2
Trisopterus luscus	0.28	T, S^2
Syngnathus rostellatus	0.30	S^2, T, S
Pomatoschistus microps	0.55	T, T^2, Tu, O^2
Pomatoschistus minutus	0.45	O^2, O, T^2, T, Tu, Tu^2, S
Pomatoschistus lozanoi	0.22	S, T, T^2, S^2
Pleuronectes platessa	0.27	Tu, S, T^2
Limanda limanda	0.58	T^2, O^2, T, O, Tu, S, Tu^2, S^2
Platichthys flesus	0.51	S, O, O^2, S^2, T
Solea solea	0.37	S, S^2, T, T^2
Liocarcinus holsatus	0.54	S^3, S, T^2, O^2
Carcinus maenas	0.54	S, T, Tu
Crangon crangon	0.22	O^2, O, T

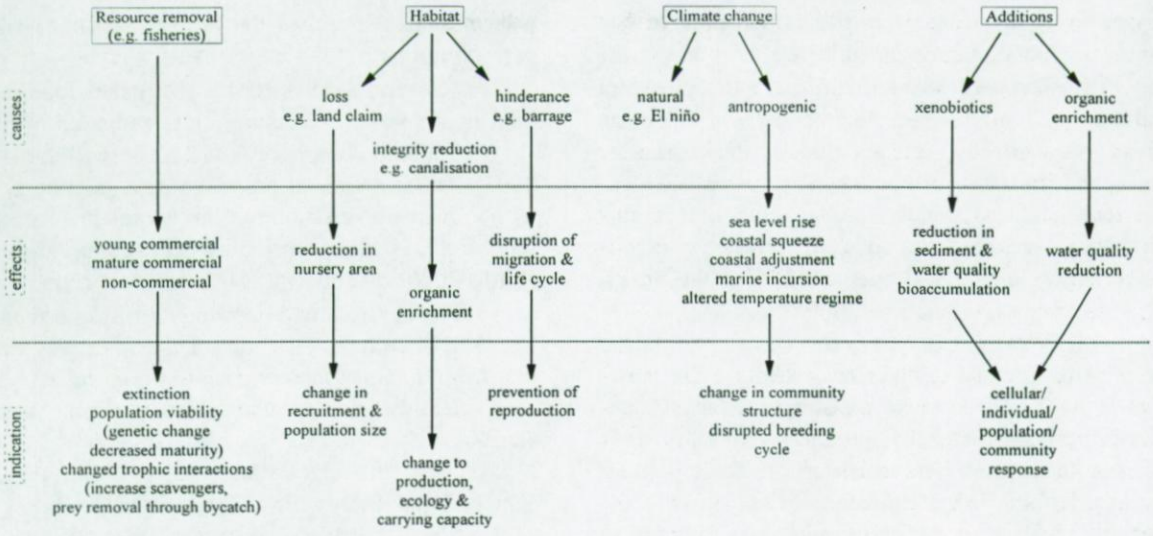


Fig. 9.13 Schematic overview of human impact on environmental changes and on the fish and macro-invertebrate assemblages (after Elliott 2002)

and *Liocarcinus holsatus*, partially repressing the effect of the other environmental variables in these models. *Limanda limanda* and *Pomatoschistus minutus* showed a different seasonal distribution pattern in the Oosterschelde, which could not be predicted by the Westerschelde models. Perhaps for *L. limanda* a distinction should be made between the different cohorts (0- and 1+ groups). Also, it could be that the Westerschelde models are less useful in the Oosterschelde, as some of the environmental variables found in the Oosterschelde are at the limit (even outside the limits for turbidity) from the ranges found in the Westerschelde.

There has been much discussion about the relative importance of environmental and biological factors in regulating natural populations, where environmental variables are associated with stochastic fluctuations, and biological ones with deterministic regulation (Sugihara *et al.* 1990). Probably other variables are needed to improve the prediction of density in both systems.

9.7 Human impact

Up till now we have tried to relate structural patterns in biodiversity, occurrence and density to the environment. Throughout this overview we briefly touched upon the impact of human activities on the integrity of the demersal fish and macro-invertebrate assemblage and on the estuarine environment in both estuaries.

Human impact can be grouped in general terms as additions (of pollutants, diseases, structures) or as removals (of space as area or volume, and of physical or biological components) (Elliott 2002). Hence, the major threats to estuarine fish and macro-invertebrates can be summarized as follows: (1) overfishing and the ecosystem effects of fisheries; (2) modifications to the habitat and the effects of climate change; (3) the repercussions of polluting inputs, including chemical, biological and physical inputs to the system (Fig. 9.13).

Resource removal through overfishing usually takes place outside the estuary, and may lead to a reduced population viability and changed trophic interactions, leading to a decreased input of juveniles into the estuarine nurseries. Habitat reduction and disturbance may decrease the carrying capacity of a system. Most probably, the dredging activities in the Westerschelde contributed to the decreased densities in 2000-'01. Hinderance mainly leads to a decrease in diadromous species (Maes 2000), but is of less importance in the Westerschelde. Also, the engineering works in the Oosterschelde may have led to temporarily changes, but a decade later the fish and macro-invertebrate populations reverted to pre-barrier densities (Hostens *et al.* 1993, Chapter 4).

Additions of alien species may have a negative impact on the native populations, as is the case in the Oosterschelde for a number of crab species (Chapter 5). Organic enrichment and the subsequent oxygen depletion are known problems in the upper part of the Schelde estuary, but this will probably only have a minor effect on the fish and macro-invertebrate distribution in the Westerschelde, as dissolved oxygen concentrations rarely dropped below 5 mg l^{-1} throughout the whole study period of the present thesis in this part of the estuary (Chapter 6). Moreover, the water quality in the upper part of the Schelde has improved during the past decade through waste water treatment and the reduction of nutrient inputs (Van Damme *et al.* 1999).

Problems with chemical pollution may be more of concern in the near future, linked to an im-

proved oxygen balance in the upper part of the Schelde estuary. Although, little is known about the fate of this type of pollution in the estuary, except that they are bound to fine sediments (Van Eck *et al.* 1998). As such, they are not directly dangerous for fishes and macro-invertebrates. Still, there is a general lack of basic understanding about the various toxic substances, *e.g.* the complexes of heavy metals and micropollutants that may be formed due to increased oxygen levels (Little 2000).

Human impact surely has contributed to the diminishing quality of the Dutch Delta area. However, it is difficult to make a distinction between human impact and natural population variability. It is still not known how and at which life stage population regulation works (Rijnsdorp *et al.* 1991). Most probably, long-term and expensive data monitoring are needed to fully understand this problem.

9.8 A generalised food web of the Westerschelde

Next to the structural forcing environmental variables, the nursery function is largely dependent on food availability. In an early assessment, it was noted that generalised estuarine food chains are basically fuelled by either phytoplankton or detritus as a source of energy (de Sylva 1975). Recent studies proved that microphytobenthos, dissolved organic matter, bacteria and microfauna (the so-called microbial loop) are likely to be the starting point of the food chains, especially in turbid estuarine environments (Billen *et al.* 1990, Heip *et al.* 1995). However, it is as yet not clear which factor really contributes most to the rest of the food chain (P. Herman, pers. comm.).

Several studies have constructed food webs of fish assemblages in estuarine systems, all of them showing a high complexity (overview in Elliott *et al.* 2002). The generalized food web presented here, has by no means the intention to be 'complete'. Building food webs is time consuming and labour intensive (Little 2000). Surely, not all biological components are studied or taken into account, and links are partly based on literature. The present thesis largely benefits from complementary research on other biotic compartments in the very well studied Westerschelde.

Still, the relative importance of each component and the energy flow between them is not included (*e.g.* Baird & Ulanowicz 1993). Either the data on production/consumption do not exist, or those data largely suffer from conversion problems at several steps of the calculations (see Gerking 1994). First, there is the problem of net-efficiency in the calculation of densities and growth (see Chapter 1), and the gravimetrical conversion to biomass/production units. Secondly, there is the problem of consumption calculations by means of experiments on gut-passage time, daily rations, and the gravimetrical conversion of food-items. Thirdly, there are problems of upscaling from experiments to the field, from small areas to large areas, and even from one area to another. All these factors make it almost impossible to calculate appropriate energy budgets. Several attempts led to enormous discrepancies (see Chapter 7-Add., Chapter 8)

The food web is based on that of Henderson *et al.* (1992), presenting the trophic levels from primary producers to primary, secondary and higher

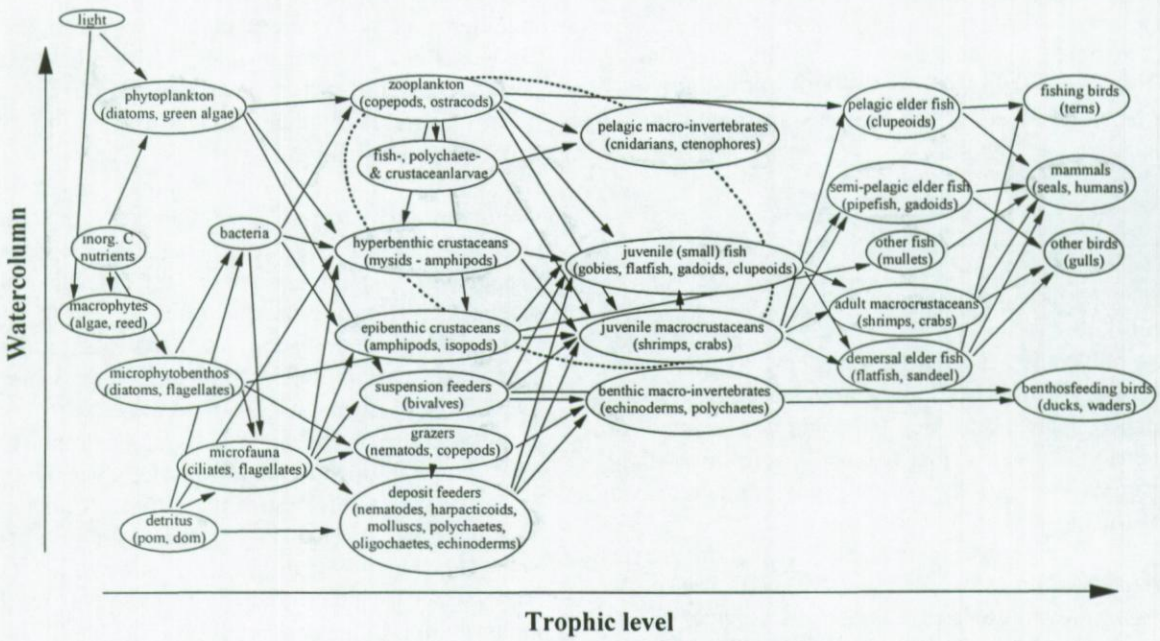


Fig. 9.14 A generalized food web for the Westerschelde estuary presenting the trophic levels along the horizontal axis, and the distribution in the watercolumn along the vertical axis. The arrows towards detritus have not been drawn for simplicity

consumers along the horizontal axis, and the distribution from benthic to pelagic in the water column along the vertical axis (Fig. 9.14). Two food webs are known to exist in the Westerschelde: an autotrophic food web in the marine part and a heterotrophic food web in the brackish part (*e.g.* Chapter 8-Add., Hummel *et al.* 1988b, Goosen *et al.* 1997). As already explained, the main source of energy in the Westerschelde is detritus (either particulate or dissolved organic carbon, Soetaert & Herman 1995a) and the bacteria/microfauna associated with it (Billen *et al.* 1990, Heip & Herman 1995, Hamels *et al.* 1998), next to micro-phytobenthos (Underwood & Kromkamp 1999, mainly in the intertidal) and phytoplankton (van Spaendonk *et al.* 1993, mainly in the marine subtidal, as this source of primary production is being suppressed due to water turbidity). The benthic primary production forms the main food source for macrobenthic (Herman *et al.* 2000) and meiobenthic (Moens & Vincx 1997) organisms intertidally, while copepods (Tackx *et al.* 1995) and mysids (Fockedey & Mees 1999) mainly use the pelagic component (subtidally). The following trophic level consists of the demersal (small) fish and macrocrustaceans (the present study), next to the benthic and pelagic macro-invertebrates. At the following level larger demersal fish and macro-invertebrates and pelagic fish are found, while the top level exists of birds (Ysebaert 2000) and mammals (including man).

In the following paragraphs it is tried to prove that the major energy flow between the secondary trophic level and the demersal fish and macrocrustaceans in the subtidal Westerschelde, passes through the pelagic rather than the benthic food chain.

9.9 The paradigm of the mysids in the Westerschelde

9.9.1 Foraging strategies

The diet of most estuarine fish species is more or less restricted to part of the total available prey spectrum as dictated by their capability to capture and ingest specific prey species. Most dietary shifts (ontogenetic, seasonal, or shifts towards the most profitable prey) are related to *e.g* the trophic adaptability of the fish species, food partitioning and/or seasonality in prey availability (Gerking 1994).

Several studies on trophic relationships have shown that estuarine fish are primarily feeding near the bottom, mainly on small epibenthic crustaceans and benthic organisms (see Elliott *et al.* 2002). In the

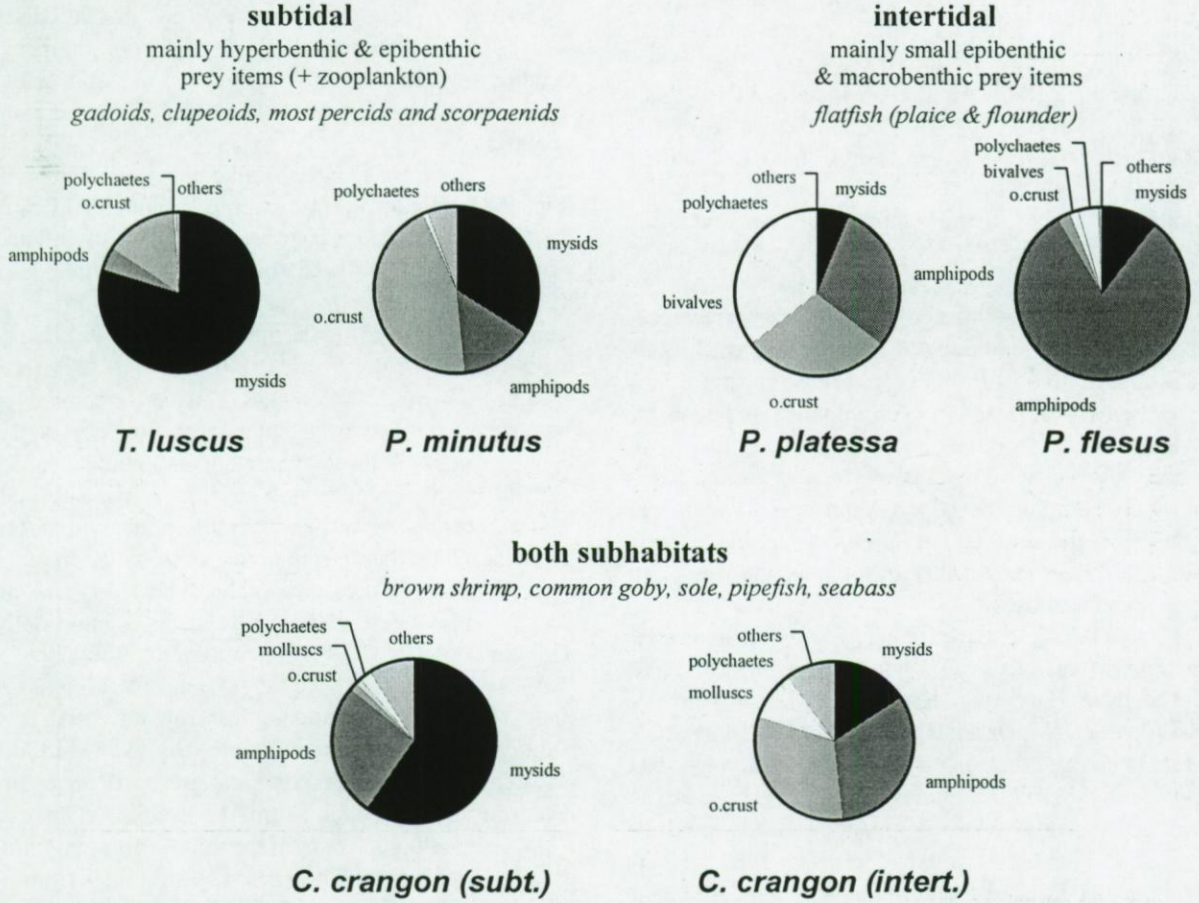


Fig. 9.15 Numerical diet composition for a number of representative species divided into three groups, based on their foraging strategies

Forth (UK) and the Tagus (Portugal) estuaries, fish feeding in the subtidal habitats were highly dependent on small crustaceans, especially shrimps and crabs (Costa & Elliott 1991). Only few studies mention mysids as important prey items for both fish and macro-crustaceans (Moreira *et al.* 1992, Marshall 1995, Oh *et al.* 2001).

The presence of an estuarine mysid-feeding guild was investigated by means of stomach content analyses on *ca.* 1500 stomachs of 25 fish species and 750 stomachs of brown shrimp *Crangon crangon*, taken from both the subtidal and intertidal habitats in several seasons (Chapter 7, Chapter 8, and K. Hostens unpubl. data). Only the main foraging patterns are presented in this overview.

The demersal fish and macro-crustacean assemblage of the Westerschelde could be divided into 3 main groups, according to their foraging strategy. A first group foraged subtidally on fast-moving hyperbenthic and epibenthic prey items (and zooplankton). Members of this group belong to the gadoids, clupeoids, most percids and scorpaenids. For example, bib *Trisopterus luscus*, got most of its energy from mysids (mainly *Neomysis integer* in the brackish zone and *Gastrosaccus spinifer* in the marine zone) and other small crustaceans. Sand goby *Pomatoschistus minutus* took 90 % crustaceans, of which almost half were mysids (mainly *N. integer* and *Mesopodopsis slabberi*) (Fig. 9.15).

A second group foraged on slow-moving epibenthic crustaceans and macro-endobenthic organisms, mainly in intertidal areas. This group mainly consisted of two flatfish species. Plaice *Pleuronectes platessa* took 70 % small crustaceans (*N. integer* and *Corophium volutator*), next to bivalves (mainly siphons of *Macoma balthica*) and polychaetes (mainly tail-ends, mostly *Heteromastus filiformes*). Flounder *Platichthys flesus* even took 90 % crustaceans (mainly *C. volutator*).

A third group showed no clear preference, feeding in both subtidal and intertidal areas. Species like common goby *P. microps*, brown shrimp *Crangon crangon*, sole *Solea solea*, pipefish and seabass, belong to this group. For example, *C. crangon* mainly preyed upon mysids (*N. integer* and *M. slabberi*) and amphipods (*Corophium* and *Bathyporeia* species) in the subtidal, and on the same prey groups but in different proportions in the intertidal, supplied with some molluscs.

The same partitioning in subtidal-intertidal feeding groups has been found in other systems, like the Medway (UK) (van den Broek 1978) or the western Irish Sea (McDermott & Fives 1995). Other studies also showed that mainly plaice and flounder used the intertidal areas to forage on amphipods, bivalves and polychaetes, while sole and dab *Limanda limanda* fed in the subtidal (McLusky 1989). However, in the Westerschelde, stomachs of *L. limanda* were always empty in the subtidal, and the intertidal sampling period was too short to figure out if dab makes use of the intertidal.

9.9.2 Resource overlap

Demersal fish and macro-crustaceans clearly use the same sources of energy both in the subtidal and intertidal, comparable with other studies (Hall & Raffaelli 1991, Marshall 1995). The term 'opportunistic feeders' is often used for many fish and macro-invertebrate species. The same can be said for most species in the Dutch Delta area.

For example, the fish and macro-crustacean assemblage was comparable between the Westerschelde and the Oosterschelde estuary. However, the Oosterschelde ecosystem is basically thriven on macrobenthic filter feeding organisms, which take away most of the primary production (*e.g.* Herman & Scholten 1990). This might explain the low densities of permanent hyperbenthos in the Oosterschelde (Mees & Hamerlynck 1992, Chavatte 2001). As hyperbenthic crustaceans were very important in the diet of most fish and macro-crustaceans in the Westerschelde, the same species will probably feed on other organisms in the Oosterschelde.

Moreover, different fish and macro-crustacean species forage both in the subtidal and intertidal areas on partly different prey items (Chapter 7, Chapter 8). As such, they may be termed opportunistic feeders. However, the present study proves that, although they may be opportunistic, feeding on whatever passes by, they are also selective, clearly preying upon the most energetic prey that pass by.

Generalized graphs like those presented in Fig. 9.15 obscure the presence of a number of prey items. Seasonal and ontogenetic shifts, mostly related with growth of the predators are not captured here (Chapter 7, Chapter 8). As the fish grows other organisms are preyed upon, mostly starting with copepods, changing to mysids, shrimp and fish (*e.g.* Chapter 7-Add.). Differences between size classes and subareas have been shown for flounder in the Seine estuary (France), where small flounder mainly preyed upon copepods and mysids in the subtidal, and on *corophium* and endobenthic organisms in the intertidal mudflats, while large flounder mainly preyed upon shrimps and crabs subtidally, and on larger bivalves and polychaetes intertidally (Bessineton *et al.* 1998). Also, common goby *Pomatoschistus microps* showed a seasonal partitioning of food resources by changing from an intertidal to a subtidal foraging behaviour (Rogers 1988). In the Westerschelde smaller common gobies mainly foraged in the intertidal saltmarsh creeks (Cattrijsse 1994), while bigger ones were mainly foraging subtidally (Chapter 7). The present thesis also showed ontogenetic shifts for sand goby *Pomatoschistus minutus* and bib *Trisopterus luscus* (Chapter 7).

9.9.3 The mysid-feeding guild

Mysids (and copepods) are a major food source for many juvenile fish and for brown shrimp *Crangon crangon* in the subtidal Westerschelde. Also, the small epibenthic crustaceans that were preyed upon in the intertidal (mainly amphipods like *Corophium* and *Bathyporeia* species) are more vulnerable to fish predation during their temporal excursions into the hyperbenthic water layer. This proves that the 'pelagic' part of the food chain is more important than the 'benthic' one, at least in the subtidal part of the Westerschelde.

Also other studies have appointed mysid-feeding guilds in the demersal fish assemblages (see Mees & Jones 1997). In the Humber estuary (UK), the food web was dominated by mysids and gammarid amphipods, with only larger flatfish feeding on polychaetes (Marshall 1995). In a Brazilian estuary, four feeding groups were distinguished, one group feeding mainly on suprabenthic mysids and copepods (Ribeiro *et al.* 1997). In a review, it was shown that 51 fish species from the North-east Atlantic preyed upon mysids (Mauchline 1980). In the Baltic ecosystem, herring and other semi-pelagic fish species also preyed upon mysids and zooplankton (Rudstam *et al.* 1992).

As already pointed out, the nursery function of a system is dependent on prey availability. Many species prey upon the same organisms. However, no food limitation could be detected. In the subtidal zone of the Westerschelde, copepods (Soetaert & Van Rijswijk 1993), mysids (Mees *et al.* 1993a), amphipods (Cattrijsse *et al.* 1993) and shrimps (Chapter 2) are very abundant. Epibenthic crustaceans and endobenthic organisms like bivalves and polychaetes are very abundant intertidally (Ysebaert 2000), and almost absent from the subtidal (Mees & Jones 1997).

From recalculations on the number of mysid in the diet and number of mysids available in the subtidal, it was shown that only a small fraction (1 % and between 10 and 35 %) of the standing stock of the mysid populations, was removed per day by the local fish and shrimp populations, respectively. This indicates that there is no top-down control on the invertebrate populations in the Westerschelde.

9.10 Final conclusions

The present thesis provides a baseline on the fish and macro-invertebrate assemblages in the Westerschelde and Oosterschelde. The thesis suggests that both estuaries play a significant role as nursery areas for several demersal fish and macro-invertebrate species. The analysis of the structure and functioning of the demersal fish and macro-invertebrate assemblages in the Westerschelde and Oosterschelde estuaries, at several spatial and temporal scales has yielded the following conclusions:

1 (Post)larvae of 17 fish and 11 macro-crustaceans enter the Westerschelde and/or Oosterschelde, mainly in spring. Only a few species were represented by high densities of (post)larvae: sprat, herring, 3 gobiid species, sole and flounder in all subhabitats (the latter not in the Oosterschelde); brown shrimp, shore crab and flying crab in both estuaries (the latter not in the marsh creeks); and also spider crab and anomuran crabs in the Oosterschelde. The intertidal saltmarsh creeks proved to be very important for the postlarvae of brown shrimp, clupeoids, gobies and flounder. As yet, the importance of intertidal mudflats and puddles on the sandflats for postlarvae is unknown

2 In total 96 fish species have been recorded during the last two decades, 75 species in the Oosterschelde and 74 in the Schelde estuary (including the tidal zone upstream of the Westerschelde). On a shorter time scale, only 32 fish and 6 macro-invertebrate species were recorded in the Westerschelde, with on average 16 fish and 3 macro-crustacean species per season. In the Oosterschelde, diversity was higher (41 fish and 31 macro-invertebrates). This was probably related with a higher habitat-complexity. Diversity is highly influenced by the occasional immigration of a large number of typical marine seasonal or adventitious species in different seasons. Salinity/turbidity, sediment/habitat type and temperature are the main structuring environmental variables

3 The maximum likelihood of occurrence (presence/absence) of 15 common species could be predicted fairly well by means of single species (multiple) logistic regression models, using only 4 environmental variables in both estuaries (temperature, salinity, dissolved oxygen concentration and turbidity, and/or their quadratic effects). The combined interaction of the different environmental variables is more powerful than the single variables to predict species occurrence, with a dominance of a seasonal rather than a spatial pattern

4 The multivariate (multispecies) approach has been shown to be a very efficient and powerful technique to summarize structural patterns in large multispecies data sets, either based on pooled or individual sampling points. In the Westerschelde, a clear spatial separation between the marine and brackish parts was found, correlated with salinity/turbidity gradients. In both estuaries, the seasonal patterns in the fish and macro-invertebrate assemblages were correlated with temperature/dissolved oxygen concentration gradients

5 The average densities in the brackish part of the Westerschelde were higher at the end of the 1980s, but decreased overall at the beginning of the 21th century. This was probably related to dredging and dumping activities, and the subsequent quantitative and qualitative reduction of intertidal (and subtidal) habitats. In the Oosterschelde estuary, long-term differences were less obvious and probably obscured by sampling bias. Fish and macro-invertebrate densities were relatively high in the Oosterschelde (except in the central part) both at the end of the 1980s and at the beginning of 2000

6 Only few species, mainly marine juvenile and estuarine resident species, were really common in both estuaries, with the macro-invertebrates largely outnumbering the fish fauna. The main fish species belong to gobiids, flatfish, clupeoids and gadoids; the main macro-invertebrate species belong to caridean shrimp and brachyuran crabs, supplemented with echinoderms and anomuran crabs in the Oosterschelde. Spatial differences within and between both estuaries were apparent for several species

7 A clear seasonal succession of different life history stages (postlarva – juvenile – immature - adult) of different species in different subhabitats (intertidal marsh creeks - intertidal flats - subtidal) has been shown. Several estuarine resident species showed a preference for the warmer (summer-resident species) or colder seasons (winter-resident species). Most of the marine juvenile species appeared at varying times (summer, winter or bimodal species), and stayed only for a short period in the estuaries, mostly with peak densities in spring-summer

8 Prediction of single species abundance, by means of multiple linear regressions constrained by four characteristic environmental variables (temperature, salinity, dissolved oxygen concentration and turbidity) was partly successful. Best models were built for 7 species that were present in the estuary for a longer period, but with only one clear density peak. Densities of these species were mainly structured by environmental patterns. Applicability of the best-fitting models to the Oosterschelde (a system without a marked salinity gradient) was limited

9 In the subtidal food webs of the Westerschelde, the major energy flow between the secondary trophic level and the demersal fish and macro-crustaceans, passes through the pelagic food-chain. Small crustaceans (copepods, mysids, amphipods) constituted the main diet component, with an overall dominance of mysids. There is no top-down control on the mysid populations

10 The demersal fish and macro-crustacean species showed different foraging strategies. Two flatfish species (plaice and flounder) mainly foraged in the intertidal on amphipods, bivalves and polychaetes. In the subtidal, most juvenile fish species (all gadoids, clupeoids, scorpaenids, percids, and other flatfish species) and brown shrimp mainly preyed upon mysids, amphipods and copepods. Some of these (*e.g.* sole, common goby, seabass, pipefish and brown shrimp) also foraged in the intertidal, mainly on amphipods. There is a large resource overlap, but also ontogenetic and seasonal shifts in the diet were observed, related with growth of the species, migration between the different subhabitats, and prey availability.

9.11 Remarks on the thesis and recommendations for future research

The papers presented in this thesis span a period of 13 years. This probably makes the thesis less coherent than if it would have been written in a much shorter period. Also our understanding of the functioning of estuaries, and of the demersal fish and macro-invertebrate assemblages in estuaries, improved during that 13-year period. Most of the research on fish and macro-crustaceans in European estuarine environments have been compiled and reviewed in the book 'Fishes in Estuaries' (Elliott & Hemingway 2002), in which I also made a contribution to several chapters. Indisputably, this has influenced the writing of the latter papers and of this final chapter.

On the other hand, the thesis benefits from the fact that three adjacent and different water bodies, a true estuary (the Westerschelde), a marine bay (the Oosterschelde) and an ebb-tidal area (the so-called Voordelta), could be compared. Additionally, at least two distinct periods (spanning more than a decade) could be compared for the Westerschelde and Oosterschelde estuaries, but unfortunately with a large gap during the 1990s.

During the 1980s (and before) much attention was given to the Oosterschelde and the Voordelta, where several research groups investigated the effects of the major engineering works (the so-called Delta plan) in an interdisciplinary approach (Nienhuis & Smaal 1994a). By the end of the 1980s most 'scientific eyes' got focused on the Schelde estuary (Westerschelde and Zeeschelde). Throughout the study period and to date, it is generally accepted that the Schelde estuary harbors a cocktail of pollutants and that the system suffers from high organic loads mainly upstream the Westerschelde (Baeyens 1998). For many system components baseline information was needed. Additionally, the importance of habitat complexity (subtidal, intertidal, saltmarsh

creeks) for the functioning of the Westerschelde as a nursery for demersal fish and macro-invertebrate species got more attention. During the mid-1990s most of the fish research in the (Dutch part of the) Delta area ceased.

Only at the end of the 1990s (after 'alarming' news from local fishermen about 'strong' decreases in fish and shrimp populations in both systems) the monitoring was repeated both in the Oosterschelde and Westerschelde. From the previous studies we knew that macro-invertebrate species were very important in these shallow areas. An increased interest in the biodiversity of the whole demersal fish and macro-invertebrate assemblages, led to the fact that since the late 1990s all macro-invertebrates (sampled with a beam trawl) have been taken into account, while during the earlier sampling periods mainly the fish and only the most conspicuous macro-invertebrates have been investigated.

Recommendation 1: future beam trawl campaigns should always concern the whole demersal fish and macro-invertebrate assemblages.

Although the different data sets were gathered through different monitoring studies (partly collected before the start of this study, but largely analyzed during the study period), they all suit the same purpose: increasing our knowledge on the nursery function of the Delta area. Of course, the constraints on the sampling (e.g. quarterly sampling, not all groups investigated, limited set of environmental variables, unknown net-efficiencies of the different gear types) and the continuous human impact on the systems, often make it not possible to reach firm conclusions.

A large part of the thesis is spent on providing descriptive baseline information, giving an idea about species composition, diversity, density and biomass of the demersal fish and macro-invertebrate assemblages, and the relation with the environment at different scales in time and space. Multivariate statistical techniques have proved to be very successful to explore and summarize that information. During the progress of the study we moved from pure descriptive ecology towards more predictive ecology, and single-species correlative models on the occurrence and density of the common species were developed. Perhaps, more progress in process studies could have been made if the descriptive study (one of the initial aims of this thesis) had been finished earlier.

Still, the major conceptual limitation of all regression techniques (either in a single or multi-species approach) is that one can only ascertain relationships (or correlations), but never be sure about underlying causal mechanisms. A number of authors find seasonality (independent of temperature or salinity) to be the main forcing factor in the distribution of migratory species (like fish and macro-invertebrates) (see Maes 2000). Still, in my opinion, the environmental conditions are of primary importance for the distribution of a number of these mobile organisms (mainly the estuarine residents). The effects of temperature on optimal growth, the avoidance of unfavorable salinities and temperatures, the effect of salinity on osmoregulation, etc., have been described by several authors (see Elliott & Hemingway 2002). The need for dissolved oxygen to survive seems obvious. Moreover, combined interactions between the environmental variables are known to influence recruitment and the migrating behavior of several fish and macro-invertebrates, and the environmental interactions can affect both prey and predator distributions.

To increase the predictive success of the density models (and the prove of causal relationships) it might be necessary to include biological factors (such as prey availability as a measure for habitat quality) or other environmental parameters (such as habitat complexity). However, it will make the models less useful, as it will be too time and money consuming to gather all necessary data. As stated in several chapters in the thesis, not many studies exist where prey abundance of several groups (hyperbenthos, zooplankton, macrobenthos) have been gathered simultaneously with epibenthic data. Moreover, the link between intertidal macrobenthos and subtidal fish data will be difficult to model directly. Also, only slightly more variance got explained by the inclusion of hyperbenthic data, mainly due to a reduction in number of sampling points that could be used. It might be interesting to try to model presence/absence and/or density of the prey organisms, and use these as predictor variables in the fish models. On the other hand, this and other studies showed that food supply is never (or seldom) a limiting factor for fish and macro-invertebrates in estuarine environments. Still, more and better multidisciplinary research is needed.

Recommendation 2: the future mainly lies in extending and fine-tuning predictive process studies. A target species might be dab Limanda limanda as this species shows different distribution patterns in the Westerschelde and the Oosterschelde, the latter system lacking typical estuarine gradients.

A major remark may be that the papers presented in this study mainly focus on the estuarine area, with less attention for what is happening both up- and downstream the systems. Of course, the distribution of fish and macro-invertebrate assemblages does not stop at geographical borders. As has been indicated in Chapter 1, we unsuccessfully tried to sample with a beam trawl upstream the Dutch-Belgian border. Although, since the 1990s data have been gathered from the upstream part of the Schelde estuary, these were taken by different sampling tech-

niques, which make these data difficult to compare with our beam trawl data from the Westerschelde. The studies from the Zeeschelde have shown an improvement in the occurrence of fish and macrocrustaceans in the upper estuary (mainly gobies, clupeoids, pipefish, brown shrimp *Crangon crangon* and prawn shrimp *Palaemonetes varians* subtidally, and sole *Solea solea*, plaice *Pleuronectes platessa* and eel *Anguilla anguilla* intertidally), but only in the Beneden Zeeschelde. The Boven Zeeschelde is still almost void of 'epibenthic' life (Peeters *et al.* 1999, Maes 2000). Also, preliminary comparisons indicate that densities upstream the Dutch-Belgian border are still much lower than in the brackish part of the Westerschelde (K. Hostens, unpubl. data).

Recommendation 3: in the future it is necessary to monitor the whole estuarine part of Schelde (and even the riverine part for diadromous species). For both systems, but especially the Oosterschelde, it might be of interest to investigate the status of fishes and macro-invertebrates in the adjacent waterbodies and upstream the rivers, in case it is decided to re-establish an estuarine gradient (from fresh to marine) in the system.

The human impact clearly diminished the quality of the Delta area, but it is difficult to judge how large the human impact really is (see §9.7). Climatological variation, year-class strength and human impact on a larger scale, largely mask the possible anthropogenic effects in the estuaries themselves. Moreover, basic knowledge on the physics (i.e. hydrodynamics and geomorphology) of the system is needed in order to interpret the biology.

Inter-annual variability in population densities forms a major constraint in establishing causal relationships. The relation between (post)larval recruitment from the spawning areas, juvenile densities in the nurseries (like the Delta area) and the adult populations (or year-class strength) in the North Sea is not yet fully understood to date. The same holds for the effects of overfishing (and/or pollution) in the North Sea on year-class strength. Yearclass data only exist for commercial species (*e.g.* cod *Gadus morhua,* herring *Clupea harengus*, or plaice *Pleuronectes platessa*) and are biased by several assumptions as well. Most probably yearclass strength is correlated with climatological changes, rather than with human impact, although the impact of overfishing on changes in the food web, and the subsequent decrease in viability of the target organisms, may not be underestimated. As can be seen from reports by the DYFS (RIVO, NL), the Wadden Sea and the Dutch coast are much larger and as such harbor much higher densities of juvenile fish. Still, it is argued that the Delta area delivers an important contribution to the North Sea stocks for a number of species living in the vicinity of the Delta area.

Recommendation 4: continuous long-term monitoring of both biological and environmental components is necessary, and full-drawn (field)-experiments are needed to assess the problems related to human versus natural changes. Especially, increasing our knowledge on net-efficiency would largely improve the interpretation of the data.

In this study, the effects of chemical (in)organic micro-pollution (mainly in the Westerschelde) on fish and macro-invertebrates are considered to be of minor importance (as these substances are now 'safely' bound to small particles). However, the (near) absence of a number of species (*e.g.* viviparous blenny *Zoarces viviparus*, starfish *Asterias rubens* and crustacean parasites of shore crab *Carcinus maenas*) seemed to be correlated with several kinds of industrial pollution. Although, the industrial and agricultural input of several pollutants has been reduced substantially during the past 30 years, in the near future more problems might arise (through bioavailability and bio-accumulation) from micropollutants. These may form suspended complexes due to increased dissolved oxygen levels (through reduced organic input and hence reduced bacterial productivity) and mixing of the water column (due to stronger currents as a result of the deepening of the shipping channel). Recently, an OSTC-project of the Belgian Federal Science Policy (ENDIS/RISKS) investigates the effects of endocrine disturbance in several organisms of the secondary trophic level (including shrimps and gobies) in the Schelde estuary.

Recommendation 5: comparison between individuals from the 'pristine' Oosterschelde and the 'polluted' Westerschelde might shed a light on the effects of industrial and agricultural pollution.

Another problem is the quantification of the carrying capacity of a system, i.e. how many resources (both food and space) are available and how many of these resources are used by the demersal fish and macro-invertebrate assemblages. As stated several times, intertidal habitats (saltmarsh creeks, sand or mud flats) are crucial for the presence of both demersal fish and macro-invertebrates, mainly as foraging and refuge areas. Moreover, it has been shown that 14 fish species might spawn in the Westerschelde, although no hard information exists for most of them. It would be interesting to have better information on (post)larval entrance and the use they make of the intertidal sand- or mudflats.

Recently a long-term vision on the Schelde estuary has been created by the Dutch and Flemish governments (Resource Analysis 2001). A major topic is 'naturalness', with the preservation of morphology and habitat complexity as the main aim. Throughout the thesis, it has been shown that the

areal extent of intertidal habitat decreases both in the Westerschelde and Oosterschelde estuaries. Moreover, (almost) nothing is known on the usage of the large intertidal mudflats throughout the systems or the sandflats in the marine part of the Westerschelde. Also, no recent intertidal data from the Oosterschelde exist. It would be interesting to know how the controlled inundation areas in the upper part of the Schelde estuary will get populated by the fish and macro-invertebrate assemblages.

Recommendation 6: the study of the nursery function would largely benefit from an increased understanding of the early life history stages of both fish and macro-invertebrates. The functioning of the intertidal habitats for fish and macro-invertebrates should be investigated in more detail, both on a macro- and microscale (e.g. extent, 'distance' from the subtidal, current regime, sediment characteristics, shape of the slopes). This might help to generate better estimates of the carrying capacity of the different systems.

Moreover, not only the quantity but also habitat quality is important. During the three last sampling campaigns in the Westerschelde (May, August and November 2001) the subtidal sediment seemed to be coarser throughout the system (although this was not confirmed by analyses), where in previous campaigns shell fragments (and peat) used to be limited to a small part of the Westerschelde. A possible correlation between coarse sediments and decreased densities in the demersal fish and macro-invertebrate assemblages at the beginning of the 21th century can be made. However, it remains unclear if this coarser sediment was only a temporarily phenomenon. A link with the excessive dredging (partly due to the extra deepening of the navigation channel) seems obvious, but should be explored further.

Decreasing fish densities in the eastern part of the Oosterschelde in 2000-'01 were attributed to a reduced habitat quality, due to more wild oysters (reducing the areal extent of soft sediments) and the increased presence of (drifting) macrophytes. A link with the engineering works (and the reduced freshwater input, next to lower current velocities) seems obvious. Also, several so-called alien species invade the coastal and estuarine waters. It might be interesting to look at the effect of global warming on habitat quality and on changes in the geographical distribution of 'new', 'sporadic' and 'common' species.

Recommendation 7: in the future, it might be worth to found the possible correlations between habitat quality and global warming and demersal fish and macro-invertebrate densities.

Since the 1980s progress has been made in the elucidation of food webs, in estuaries and the Westerschelde in particular, through this and other studies. The basic idea of two food chains in the Westerschelde (autotrophic in the marine part and heterotrophic in the brackish part) established by Hummel *et al.* (1988b), remains valid to date. Although, the importance of detritus as the main food source for the lower trophic levels in the heterotrophic food-chain seems to be smaller than previously thought.

The functional part of this thesis mainly tackles the identification of the main food sources and foraging strategies. Food availability and feeding ecology have always been central themes in the Marine Biology research group at Ghent University. At the end of the 1980s mysids were 'discovered' as a very important food source for fish in the Delta area. Many studies and projects have been developed to unravel that part of the food-chain.

The seasonal appearance of different species might lead to a fully realized carrying capacity throughout the year. However, most of the food resources seem to be not used (e.g. only 30 % of the mysid standing stocks is consumed per day) and almost nothing is known of predation impact by fish on macrobenthic organisms in the Delta area. Most probably, the carrying capacity of the system is not optimized, but as yet unknown. Because of limited information (and lots of assumptions) on gastric evacuation rates, daily rations, secondary production, P/B and P/C ratios, also the production and consumption estimates reported in the different chapters of the thesis are preliminary and should only serve as baseline information for the area concerned. Large discrepancies are found between consumption values based on stomach content analyses and real calorific needs of the demersal fish and macro-invertebrates.

Recommendation 8: more detailed investigation of the diet of different macro-invertebrate and fish species in the Westerschelde and the Oosterschelde should be encouraged. The latter system seems to be completely dominated by the benthic food-chain where the secondary production is mainly delivered by bivalves and polychaetes intertidally. This is in contrast to the Westerschelde, where the pelagic food-chain (secondary production mainly delivered by copepods and mysids subtidally and amphipods intertidally) is very important, as has been shown in this thesis. Estimating reliable consumption rates for the investigated species will require further validation with extensive sets of experimental data.

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ZULLEN WE HET ŒUVRE DAT JE OOIT HAD WILLEN SCHRIJVEN MAAR WEGDOEN?